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The Ontogeny of Red Wolf *(Canis rufus)* Social Behavior: Implications for Sociality and Taxonomic Status

Tarren Kay Wagener
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Tarren Kay Wagener entitled "The Ontogeny of Red Wolf *(Canis rufus)* Social Behavior: Implications for Sociality and Taxonomic Status." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Life Sciences.

Michael R. Pelton, Major Professor

We have read this thesis and recommend its acceptance:

Gordon Burghardt, John Gittleman

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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The Ontogeny of Red Wolf (*Canis rufus*) Social Behavior: Implications for Sociality and Taxonomic Status

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Tarren Kay Wagener

December 1998

Dedication

This thesis is dedicated to the two most important men in my life:

my brother, Joel, who has been my strength while completing this degree,

and to my father,

Dr. John Wayne Wagener,

who was undoubtedly the most courageous and incredible man I will ever know.

I completed this thesis in honor of you. I wish you could have read it.

Acknowledgments

This project would not have been possible without the support of numerous organizations and individuals. First, this project was generously funded by the United States Fish and Wildlife Service through the Point Defiance Zoological Park and Aquarium. For this, I am indebted to both Gary Henry, Red Wolf Recovery Coordinator and Will Waddell, Red Wolf Species Survival Plan Coordinator. Both the Knoxville Zoological Gardens and Fossil Rim Wildlife Center allowed observations of their wolves at all hours and I would like to thank Greta McMillan, Kelley Snodgrass and MaryJo Sterns. My graduate committee, Drs. Michael Pelton, Gordon Burghardt and John Gittleman, provided significant direction and innumerable insights. Additionally, they supported my non-traditional degree plan and I am sincerely thankful for their support in that regard.

Many individuals throughout my academic and work experiences have been instrumental in my decision to complete the graduate degree. Drs. Robert Lickliter and Joseph Franchina at Virginia Tech first exposed me to behavioral research and encouraged me to pursue an advanced degree. Numerous individuals in the zoo field have been a significant source of inspiration, specifically Drs. Jill Mellen, Cheryl Asa, Tom Foose, Susie Ellis, Mike Hutchins and Mr. Jack Grisham. Additionally, I would like to acknowledge wolf biologists Mike Phillips, John Weller, Chris Lucash and Jennifer Gilbreath for their support and numerous conversations regarding red wolf behavior. It is only through their and others' dedicated efforts that the red wolf continues to thrive in the wild. Lastly, I would like to sincerely thank Dr. Marc Bekoff for both his friendship and the work which served as a model for this project. He has provided invaluable comments related to the development of canid behavior.

This thesis would not have been the product it is without the editing skills of Holly Emery, Fort Worth Zoo (FWZ) Conservation Assistant, who served as an excellent employee and an even better friend. Michael Fouraker, FWZ Director of Animal Collections, provided tremendous support through the flexibility to complete the degree while also allowing me to maintain my position at the Fort Worth Zoo.

Finally, I would like to thank my family, Linda, Jon, Jack, Barbara and particularly Joel, who maintained faith in my abilities even when I did not. This thesis is a testament to their constant love and support.

Abstract

Patterns of behavioral development in closely related North American *Canis* have been studied extensively. Developmental trends have been used to assess species-typical social organization and taxonomic relationships in wolves (*C. lupus*), coyotes (*C. latrans*) and domestic dogs (*C. familiaris*). Despite its species designation, the taxonomic status of the closely related red wolf (*C. rufus*) is fiercely debated and a hybrid origin (*C. lupus* x *C. latrans*) has been proposed. The objective of the current study therefore was to analyze growth and behavioral development patterns in the red wolf and perform general comparisons to trends previously documented in wolves and coyotes.

Two captive born red wolf (*Canis rufus*) litters (litter 1: n=5 pups, 2 adults; litter 2: n=4 pups, 2 adults) were observed from 28-50 days of age. Data were collected on the form, frequency and duration of select pup-pup and pup-adult social interactions as well as pup-object play. Growth patterns and trends of physical development were also examined in litter 1.

Growth patterns were consistent with that reported for other closely related canid species: age at eye-opening, age of independent urinary and defecation control, and the consumption of solid food were similar to that documented for wolves and coyotes. Red wolf pup weights were intermediate to that described for wolves and coyotes. Teeth erupted on average later and in a different order than that previously described in coyotes.

Observed behavioral trends were intermediate to that of coyotes and wolves and shared characteristics of each. The form of pup behavior patterns did not differ qualitatively from that previously documented for either gray wolves or coyotes. However, pups simultaneously exhibited"species-specific" behavior patterns previously attributed to both wolves (leap leap, prolonged jaw wrestling) and coyotes (inguinal response, defensive gape). Early red wolf social interactions were predominantly agonistic and primarily in the form of threats rather than overt aggression. There was no evidence of a dominance hierarchy in either litter. In both litters, the frequency of play increased concurrently with a decrease in frequency of agonistic interactions. Individual differences were not noted in the frequency of play or aggression in either litter; however, the two litters differed significantly in the frequency of play and aggression.

Object play followed the differential development of play and aggression. Early object play was non-

social (pup-object) and peaked during the transitional period during which the frequency of aggression was decreasing and social play increasing. Social object play (pup-pup-object) was observed later in development as reciprocal social play also increased.

Adult-pup interactions varied by litter. In general, pups spent more time in proximity to the female than the male throughout the study period in both litters; however proximity to each adult changed over time. Initially, pups spent more time in proximity to the female. As pups aged, the amount of time spent in proximity to the female decreased while proximity to the male and both the male and female increased. In litter 1, adult-pup agonistic interactions were observed almost to the exclusion of other interactions. Conversely, investigative and affiliative interactions predominated in litter 2. In both litters, male-pup interactions were frequent.

In sum, the patterns of physical and behavioral development in the red wolves observed in this study share similarities with both gray wolves and coyotes. Therefore, the data presented do not exclude a hybrid origin hypothesis. Suggestions for further research include the development of play and agonistic action patterns from days 21-28 as well as post 50 days of age, further investigation of subtle indicators of dominance and increased numbers of subjects.

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Chapter 1
Introduction

Behavioral Development in *Canis*

The development of social behavior has been studied extensively in canids. Developmental patterns have been linked to adult reproductive success, dispersal patterns and species-typical social organization (Bekoff 1977a; Bekoff 1977b; Bekoff et al. 1981; Biben 1983; Bekoff et al. 1984; Bekoff and Byers 1985; Bekoff 1989). Additionally, behavioral phenotypes expressed during development have also been used to assess or establish taxonomic relationships among closely related species (Bekoff 1972a; Bekoff et al. 1975; see review in Bekoff 1977a). North American *Canis* species in particular (*C. familiaris*, *C. lupus* and *C. latrans*) have been the focus of much of this research due to their close phylogenetic relationship, playful nature and varied social lifestyle (Kleiman 1967; Scott 1967; Bekoff 1972; Bekoff 1978; Bekoff 1989).

In general, *Canis* development has been categorized into four stages: the neonatal period (birth - 2 weeks of age; maturation of the nervous system), the transitional period (2-3 weeks of age; rudimentary adult behaviors appear), the socialization period (3-12 weeks of age; social relationships are established) and the juvenile period (12 weeks to sexual maturity; social independence is achieved) (Scott & Fuller 1965; Bekoff 1978). Despite sharing common developmental stages, it has been demonstrated that even closely related *Canis* species differ significantly in the form and frequency of behavior as well as the time course of socialization (Scott & Fuller 1965; Snow 1967; Silver & Silver 1969; Bekoff 1972; 1974a; Bekoff 1974b; Fox 1978; Willkomm 1990; Biben 1983).

The basic behavioral repertories of *Canis* species are almost identical (exceptions noted below), although the relative frequency of some acts varies across species (Scott 1967; Bekoff 1974a; Bekoff 1974b; Bekoff 1978). In general, the less social North American canids (e.g. coyotes) show more rapid motor development than wolves or domestic dogs (Bekoff 1978). The relative frequency of aggressive vocalizations, defensive gapes and passive submission is higher in coyotes than in same aged beagles or wolves (see Table A-1 for behavioral definitions). Conversely, wolves and domestic dogs engage in much more "sexual play" (mounting with pelvic thrusting) than do coyotes. Additionally, several species-specific action patterns have been documented (e.g. leap leap (wolf) and inguinal response (coyote) (Bekoff 1972;

Bekoff 1978). In general, (with the exception of sexual play), there do not appear to be any sex differences in the development of *Canis* behavior.

In addition to the differences in the frequency of occurrence of specific action patterns, there are marked species differences in the ontogeny of social interaction in *Canis* during the third-seventh week of development. Coyotes exhibit serious rank-related fighting during the fourth to fifth week of development and do not interact "playfully" until a dominance hierarchy is established (Bekoff 1974a; Bekoff 1981). Conversely, wolves play early in development (Bekoff 1974a) and do not show rank-related aggression until at least 6 months of age or older (Mech 1970; Zimen 1982). Table 1 outlines the patterns of behavioral development that have been used to differentiate wolves and coyotes.

Parent-Offspring Behavior in *Canis*

Canid parents provision for and protect young. Direct care may include resting and huddling with young, grooming and cleaning, carrying, retrieving, providing food, defending babysitting and playing or socializing with offspring (Malcolm 1985; Kleiman & Malcolm 1981). Indirect care includes behaviors which could benefit offspring even if there was no direct interaction between the adult and young, such as den construction, giving alarm calls and maintaining a territory (Malcom 1985). Through both direct and indirect interactions, canid parents are thus a substantial factor in the socialization process (Hofer 1981). In any given social interaction, the behaviors of pups with an adult depends on the adult's usual behavior towards the pup as well as the context of the interaction. Persistent patterns of parental care though, combined with ecological factors, may contribute significantly to species-specific social organization (Fentress et al. 1987).

Much has been documented on both paternal care and adult-pup interactions in North American *Canis* (Mech 1970; Bekoff 1978; Bekoff & Wells 1980a; Bekoff & Wells 1980b; Fentress & Ryon, 1982; Fentress et al. 1987). While patterns of parental care differ between the closely related gray wolf and coyote, few detailed data exist on parental behavior in red wolves.

Among coyotes, care of the young is primarily accomplished by the female, with the sire and non-breeding helpers feeding the pups rarely (Bekoff & Wells 1980a; 1980b). In captivity, Bekoff (1978) determined that agonistic interactions between parents and offspring occurred almost to the exclusion of playful inter-

Table 1. Documented species differences in gray wolf and coyote behavioral ontogeny

Behavior	Gray Wolf	Coyote
Behavioral Repertoire		
Sexual play	Frequent; can appear as early as 4 weeks of age [2,3]	Infrequent; does not appear until 14-15 weeks of age [2,3]
Marking behavior	Observed as reach sexual maturity [1]	First observed from 94 days-44 weeks of age (leg-lifting in males); 22-44 weeks (scrape marking) [2]
Inguinal response	Very infrequent [2,4]	Frequent; a species-specific behavior [2,4]
Leap-leap	Observed infrequently; a species-specific behavior [2,4]	Never observed; not part of the species behavior repertoire [2,4]
Agonistic Behavior		
Timetable	Follows development of social play [1,2,3]	Precedes development of social play [2,3]
Form	Ritualized threat behavior; limited severe fighting [1,2,3]	Severe aggression; bites uninhibited [2,3]
Passive submission	Frequent [1,2,3]	Rarely observed [2,3]
Active submission	Frequent [2]	Rarely observed [2]
Aggressive vocalization	Infrequent [2,3]	Frequently observed; days 21-28 particularly [2,3]
Defensive gape	Rarely observed [1,2,3]	Frequent [2,3]
Rank-related aggression	Not observed prior to 50 days of age (occurs during latter part of first year) [1,2,3]	Observed during 4-5 weeks of age [2,3]
Standing over	Observed in both playful and agonistic contexts [2,3]	Observed predominantly in agonistic contexts [2,3]
Social Play Behavior		
Timetable	Precedes development of agonistic behavior [1,2,3]	Follows development of agonistic behavior [2,3]
Use of play intention signals	Precede play bouts with play intention signals 30% of the time [2]	Precede play bouts with play intention signals 90% of the time [2,3]
Rank-related play soliciting ability	N/A; no dominance heirarchy present at this age [1,2]	Higher ranking individuals less successful in initiating play than lower-ranking ones [2]
Dominance Heirarchy	Established later in development; post 50-days [1,2,3]	Established early in development by agonistic encounters [2,3]

Sources:

1 Mech, L.D. 1970. The Wolf: Ecology of an Endangered Species. New York: Natural History Press.

2 Bekoff 1972. An ethological study of the development of social interaction in the genus *Canis*: A dyadic analysis. Ph.D. dissert., Washington Univ., St. Louis, Miss.

3 Bekoff 1978. Behavioral development in coyotes and Eastern coyotes. In: M.Bekoff, ed. Coyotes: Biology, Behavior and Management, pp. 97-126. New York: Academic Press.

4 Fentress & Ryon 1982. a long-term study of distributed pup feeding in captive wolves. Pp. 238-261 In: F.H. Harrington and P.C. Paquet eds. Wolves perspectives of behavior, ecology and conservation. Park Ridge, NJ: Noyes Publications.

actions. Fentress et al. (1987) noted affiliative interactions such as muzzle-muzzle contacts, tail wags and paw-raising between coyote pups and adults; however, specific playful interactions were not recorded.

Parental care in captive and wild wolves has been documented as more communal, with all pack members, including the sire, helping to feed the young (Mech 1970; Zimen 1982). Furthermore, adult (male and female)-pup playful interactions have been widely documented (Mech 1970; Fentress & Ryon 1982).

Object Play

Interactions with the physical environment are also an important component of socialization in young mammals. The proposed functions of play in general varies (Loizos 1966; Bekoff & Beyers 1981; Fagen 1981), though object play is commonly considered a distinct category of play (Burghardt 1984; Bekoff & Beyers 1981). Object play may result from boredom or vacuum activity, or may serve a function, such as species-specific predatory training (Biben 1982; Martin 1984). Additionally, interspecific variations in the form of object play have been related to species-specific prey recognition (Rasa 1971) and treatment of prey as well as social organization (Biben 1982). For example, the behavioral repertoire of the highly social bush dog was found to be more limited than those of the maned wolf and crab-eating fox (Biben 1982); however a high frequency of group object play and noncompetitive pup-object activities was hypothesized to correlate with the species' group hunting and sociality.

No data exist on the ontogeny of object play in red wolves. Furthermore, few studies have evaluated the development of the form and frequency of object play in relation to the time course of the development of non-object social interactions, both agonistic and playful. Such studies, particularly in a species in which there exists a differential time course in the development of play and aggression may help elucidate the role of object play in the socialization of the species.

The Red Wolf

Extensive controversy surrounds red wolf taxonomic status (Wayne & Jenks 1991; Wayne & Gittleman 1995) and the continued federal protection allotted to *C. rufus* and to hybrid species in general (Gittleman & Pimm 1991; O'Brien and Mayr 1991). Previous systematic approaches have resulted in conflicting conclusions concerning the taxonomy of *C. rufus* (Lawrence & Bossert 1967; Atkins & Dillon 1971; Paradiso & Nowak 1971; 1972; Wayne & Jenks 1991). Evaluations of red wolf taxonomy have used various techniques and include gross physical size and form, skull and brain morphology, vocalizations,

chromosomal karyotyping, both mitochondrial and nuclear DNA as well as general ecological and behavioral considerations (see review in Wayne et al. 1998). Goldman (1937), however, concluded that the red wolf was a distinct species and despite renewed controversy emphasizing a probable hybrid origin (*C. lupus* x *C. latrans*) (Wayne & Jenks 1991; Roy et al. 1994; Wayne et al. 1998), red wolves are currently identified as a distinct canid species.

Data on both the ecology and general behavior of red wolves is somewhat limited. Shaw (1975) determined group size for red wolves to be from 1-7 individuals. In light of this large group size range, researchers had originally speculated that the social organization of red wolves was between the predominantly though sometimes solitary coyote and the tightly pack-oriented gray wolf (Phillips, pers. comm.). More recently, however, due to preliminary results from the Alligator River National Wildlife Refuge reintroduction site (Phillips & Henry 1992), red wolf social organization seems to be very similar to that documented for gray wolves (Mech 1970). Reintroduced red wolves are occupying and maintaining territories, engaging in agonistic encounters with strange conspecifics resulting in wolf-wolf mortality, and feeding on large prey such as white-tailed deer. It has also been documented that yearling and 2-year old wolves restrict their movements to their natal home range, associate with their parents, and assist with pup-rearing. Shaw (1975) concluded that red wolf groups were predominantly unstable, and numerous cases of intraspecific mortality in the wild have been documented by recovery personnel (G. Henry pers. comm.). General behavioral data on red wolves are extremely limited and include only the angle at which the tail is held, running style, bedding preference and facial expression during threat postures, and finally aggression levels at traps (Paradiso & Nowak 1972; Shaw 1975).

No data currently exist on the development of red wolf social behavior. A general analysis of the development of red wolf social behavior then may be useful in not only elucidating taxonomic relationships among the closely related canids (wolf, coyote and red wolf), but also in analyzing developmental factors which may correlate with the fore-mentioned species-specific sociality.

Study Objectives

Table 1 outlines the significant differences previously documented in the behavioral development of wolves and coyotes. Using these data, the following objectives and hypotheses were established to describe the general patterns of growth and behavioral development in the red wolf:

(1) Develop an ethogram of red wolf social behavior

Utilizing established wolf and coyote ethograms (Loeven 1993; Bekoff 1972; Knight 1978, Lyndaker 1978; and Lindsey 1987) as references, a detailed ethogram was developed for red wolves. Pup-pup and pup-adult action patterns were described,along with the age at first appearance and the relative frequency.

(2) Describe red wolf physical development

The age at first eye opening, changes in weight over time and tooth eruption order were documented. The emergence of independent urination and defecation were also be documented.

(3) Describe the development of social play and agonistic interactions in red wolves

Age-specific trends in the frequency of play and aggression were documented. Analyses examined changes over time in the frequency of both play and aggression as well as relationships between the development of the two interaction types. Changes in the form of both play and aggressive action patterns over time were also analyzed as well as individual differences in frequency of play and aggression. Finally, the presence or absence of a dominance hierarchy was noted.

H_0 The form, frequency and time of first appearance of *C. rufus* behavior patterns do not differ significantly from those documented for *C. lupus* and *C. latrans*.

H_1 The form, frequency and time of first appearance of *C. rufus* behavior patterns differ significantly from those documented for *C. lupus* and *C. latrans*.

(4) Describe the development of red wolf object play

The frequency and duration of both non social (pup-object) and social (pup-pup- object) object play was documented. Additionally, the development of object play was compared to non-object social interactions (specifically the ontogeny of play and aggression).

Ho No differences exist in the frequency or form of object play between *C. rufus* and that documented for *C. lupus* and *C. latrans*. Differences indicate the following hypotheses:

1. Trends showing a rich repertoire of object play patterns, defense of objects, high frequency of solitary rather than group object play, and low frequency of object play relative to non-object oriented social interactions indicate solitary social organization.

2. Trends showing few object play patterns, sharing rather than defense of objects, and equal frequency of object-oriented social interactions compared to non-object oriented social interactions indicate grouped social organization.

(5) Describe parent-offspring interactions in early red wolf ontogeny

The form and frequency of adult-pup interactions was documented. Developmental changes in the actor (adult male or female) was examined and comparisons made between adults in the form of pup-directed activity.

Chapter 2
Methods

Subjects

Subjects were two family groups of captive red wolves housed at the Knoxville Zoological Gardens, Knoxville, Tennessee (2 adults, 4 pups) and Fossil Rim Wildlife Center, Glen Rose, Texas (2 adults, 5 pups). Table 2 lists the sexes of the animals, the identification codes used, birth origins, and ages. Pups were shaved (by zoo personnel) on the head and body using handheld grooming clippers to allow for individual identification. Pups were shaved every two weeks throughout the study period. Shaved areas averaged 5cm x 10 cm each. Adults were discriminated by markings, size and anatomical features.

Captive Management and Housing

Subjects were held in large naturalistic enclosures (Figures 1 and 2) equipped with artificial den structures. Available play items included natural objects such as sticks, logs, rocks and leaves. Animals were fed high quality protein dog food *(ad libitum*, Knoxville Zoo and Fossil Rim) and water *ad libitum*. Subjects at the Knoxville Zoo were also supplemented with Nebraska canine diet. Enclosures were maintained daily by zoo personnel at both facilities. Routine maintenance included visual inspections of all subjects, feeding, watering and cleaning the yards. Husbandry practices and diet are standardized through the Red Wolf Species Survival Plan © and did not differ significantly between locations. Zoo personnel weighed and shaved pups once weekly and visually inspected for tooth eruption from days 7 to 50 (Knoxville only). These invasive procedures were conducted without anesthesia while minimizing direct contact and handling time. Procedures were also conducted without the author present and outside of observation times to lessen effects on behavior.

Observational Methods

Subjects were observed daily from day 28 of age (Fossil Rim) and day 31 (Knoxville) through 50 days of age. Observations were conducted from April-June 1993 (Litter 2) and May-June1994 (Litter 1). Observations were conducted from approximately 1600-2100 from a location outside the enclosure (Figures 1 and 2) by the author. Focal animal sampling (continuous recording) (Altmann, 1974; Lehner 1996) of pups was conducted up to 20 minutes per animal per day. Initial observation times were much less than 20 minutes due to the fact that pups ventured outside the den for only short periods of time. The

Table 2. Age, sex and reproductive status of captive red wolves utilized in the behavioral ontogeny study

Individual (SB#)	Litter	Code	Age Class	Sex	Date of Birth	Birth Location
428	1	M2 [1]	Adult	Male	2-May-90	Manteo
390	1	F2 [2]	Adult	Female	21-May-89	Tacoma
722	1	J	Pup	Male	3-May-94	Fossil Rim
723	1	U2	Pup	Male	3-May-94	Fossil Rim
724	1	F	Pup	Male	3-May-94	Fossil Rim
725	1	B2	Pup	Female	3-May-94	Fossil Rim
726	1	T	Pup	Female	3-May-94	Fossil Rim
356	2	M1 [3]	Adult	Male	29-Apr-89	Audubon
297	2	F1 [4]	Adult	Female	29-Apr-89	Tacoma
619	2	S	Pup	Male	29-Apr-93	Knoxville
620	2	B	Pup	Male	29-Apr-93	Knoxville
621	2	U	Pup	Male	29-Apr-93	Knoxville
622	2	H	Pup	Female	29-Apr-93	Knoxville

[1] Approximately 4 years of age at the beginning of observations. This male sired and cared for another litter prior to this one (with a different female).

[2] Approximately 5 years of age at the beginning of observations. This female produced and cared for another litter prior to this one (with a different male).

[3] Approximately 4 years of age at the beginning of observations. This litter was his first successful breeding.

[4] Approximately 4 years of age at the beginning of observations. This litter was her first successful breeding.

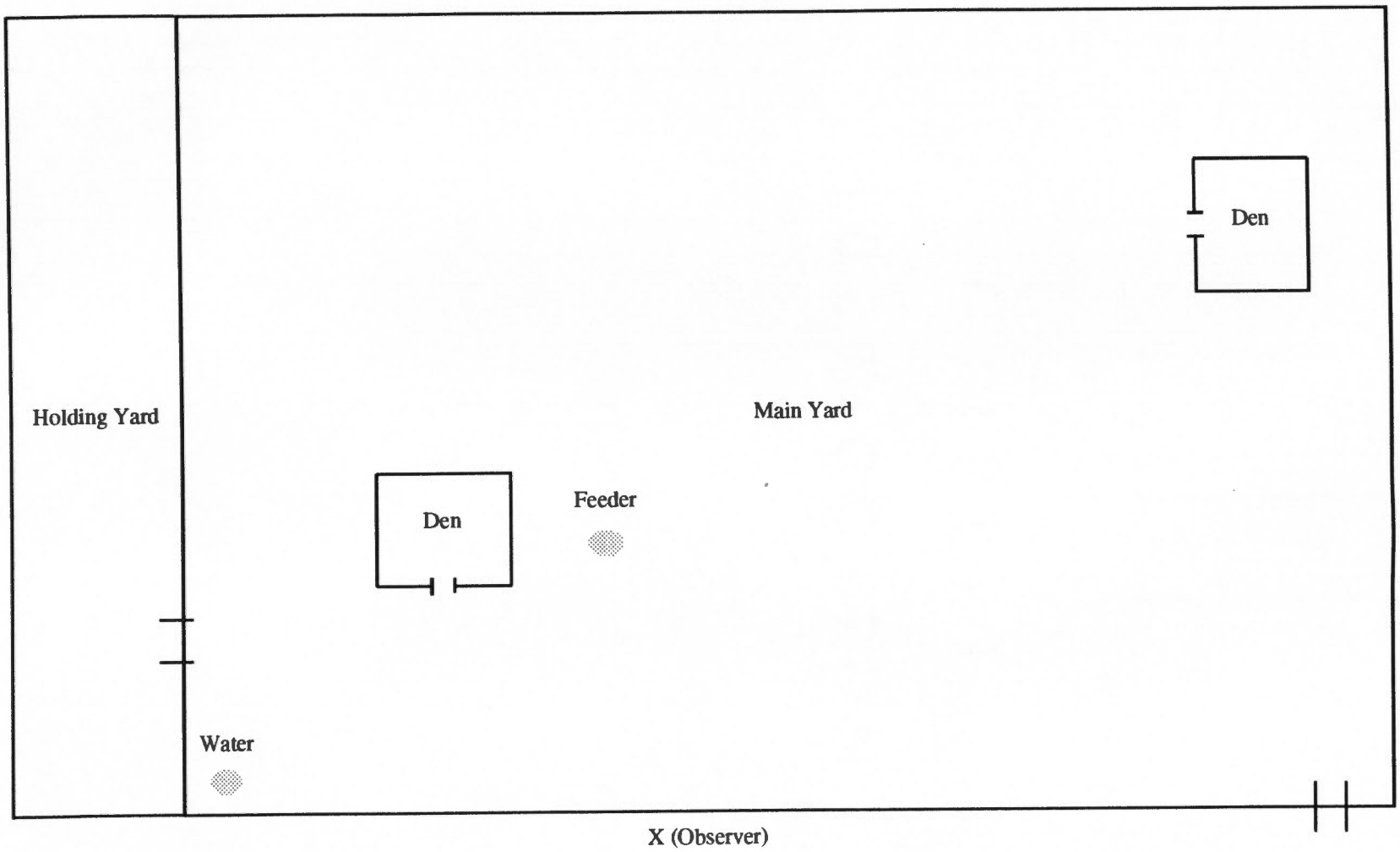

Figure 1. Schematic of Fossil Rim Wildlife Center's captive red wolf enclosure (Litter 1). (Main yard measures 115' x 55'; holding yard 20' x 20'; den structures are 5' x 4' x 3.5'. The yard substrate is primarily dirt/litter. Exhibit structures and vegetation are distributed as follows: approximately 45% brushes and small trees, 45% large trees and 10% dens. The exhibit is not open to the public (K. Snodgrass, pers. comm.))

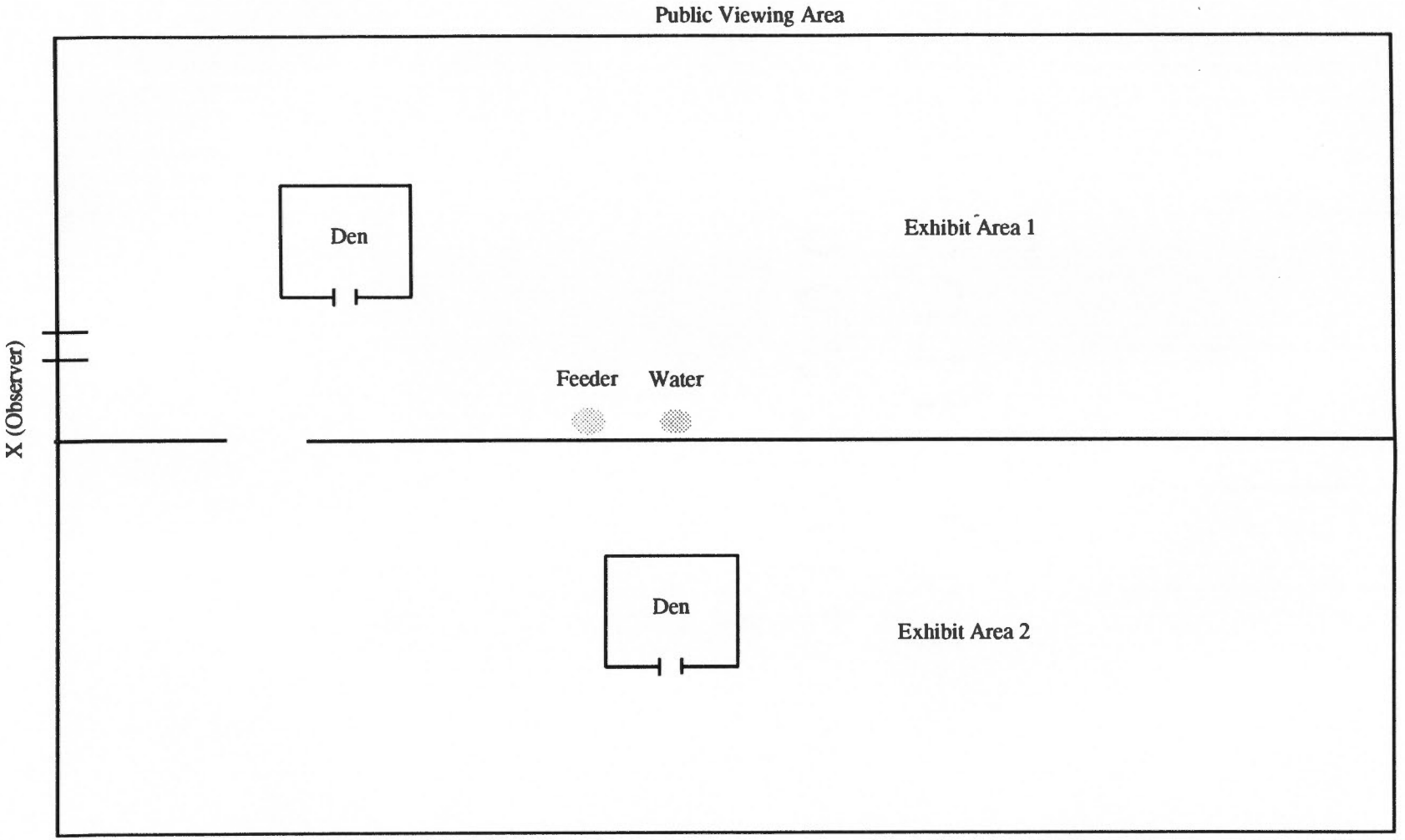

Figure 2. Schematic of Knoxville Zoo's captive red wolf enclosure (Litter 2). (Entire exhibit area measures 105' x 95'; den structures are 5' x 4' x 4'. The yard substrate is primarily dirt/litter. Exhibit structures and vegetation are distributed as follows: approximately 20% brushes and small trees, 10% large trees, 10% dens and 50% dirt mounds and elevated areas. Exhibit area 1 faces a public walkway that has a designated public viewing area 24 ft. wide. Wolves have access to both exhibit areas 90% of the time. (S. Hardin, pers. comm.))

order that subjects were observed was randomized daily and only the proportion of time that a focal animal was visible was used in analyses. There were no significant differences in the amount of time visible among individuals.

Observations were recorded with a hand-held video camera. Additional comments were made into a hand-held audio cassette player. While equipped with audio capabilities, the video camera was unreliable for recording low volume sounds such as aggressive or distress vocalizations due to the distance from the subjects and highway noise (Knoxville).

Video tapes were decoded using The Observer© (Noldus Technologies, Version 3.0), observational software to record the frequency and duration of behaviors in real-time. General notes were also recorded for each session. Behaviors observed and their definitions are listed in Table A-1. All social interactions were scored as dyadic interactions. Thus, if an interaction involved more than 2 participants, the action patterns were broken down into paired interactions. For all social interactions, the initiator, receiver, action patterns involved, and terminator were recorded. For analyses, pup-pup social interaction data were collapsed into five categories: play, agonistic, unsolicited play, general interaction and play soliciting (play + play-soliciting). General interactions included those interactions that were investigatory in nature (ano-genital investigation, Table A-1), too ambiguous to assign to a category or merely affiliative such as mutual chin resting, chewing etc. If a playful interaction (such as play-fighting) escalated into real fighting, the interaction was scored as both although the time in each category was specified. Furthermore, ano-genital investigation interactions that were clearly agonistic were scored as such. Likewise, unreciprocated play bouts in which the initial approach was rebuffed and subsequently both pups used agonistic actions (threats, aggressive vocalizations, etc.) were scored as both an unreciprocated play bout as well as an agonistic interaction. If the pup that initially solicited play turned away following the rebuff rather than escalate the interaction to a fight, the interaction was scored as an unreciprocated play only.

Pup-adult proximity data (proximity scored as within 1 body length or approximately 5 feet of dam, sire or both) were recorded in relation to the focal pup. Pup-adult interactions were categorized as general affiliative (play-soliciting, pup-directed general body bites, muzzle-muzzle contact, face-licking), investigative (ano-genital investigation, sniffing) or agonistic/disciplinary (including at least one full or inhibited bite). Adult-pup behaviors were mutually exclusive and including a null category, accounted for

100% of observation time.

Analyses

Interactive behaviors were analyzed both as frequencies (acts/total social acts) as well as durations (percentage of observed time spent in an activity). Since both play and agonistic bout lengths increase over developmental time, these statistics permitted analyses of the relative change in frequency between the categories of behavior over time. For direct comparisons with findings in previous studies (Bekoff 1972a; 1974a; 1974b; 1978), all data were lumped into three temporal periods (days of age 29-35, 36-42, and 43-50) and reported as medians. Data were analyzed both within and between litters to assess weekly trends. Friedman two-way analyses of variance by ranks tests were used to assess trends within each litter over time while the Kruskal Wallis one-way analysis of variance by rank test was used to assess differences among individuals within a litter. The Mann-Whitney U test was used to analyze sex differences. To assess differences in trends between the two litters, the Wald-Wolfowitz runs test was used. Finally, to test for differences between the male and female in parental care, the Wilcoxin matched-pairs signed ranks tests was used (Siegel, 1956; Sokal & Rohlf 1995).

Chapter 3
Results

Results are presented in the following categories: physical and early development, action patterns, non-object play and agonistic behavior, object play and adult-pup interactions. Within each category, general trends, individual and litter differences (if any) are noted.

Physical and Early Development

Quantitative physical data were obtained by the animal keepers from subjects in Litter 2 (n=4) and include length at one week, weekly weights (days 7-50, Figure 3) and tooth eruption order. Mean age at eye-opening was 13.2 days (range 12-14, s.d.=.957). Mean body length (top of head to base of tail) at seven days of age was 23.4 cm (s.d=1.6). Teeth erupted in the following order: upper canine (x=13.2, s.d=1.5), lower canine ((x=16.0, s.d.=1.4), upper (x=19.5, s.d.=1.7) and lower incisor (x=19.5, s.d.=1.0). Additionally, zoo personnel observed the first independent urination and defecation on days 7 and 17 respectively. Comparable data were not available for Litter 1.

Pups were first visible in the den entrance on day 27 (litter 2) and day 28 (litter 1). Early forays at this time were limited to either peering outside the den or stepping immediately outside the entrance for a period of time not longer than a minute. Pups in both litters were somewhat unsteady on their feet at this age; however, litter 1 animals seemed much more so. Additionally, ears of several pups in litter 1 were not fully erect until day 34. No pup-pup interactions were observed until day 32 (litter 1) and 31 (litter 2) despite the fact that they had first been visible several days earlier. On many occasions, pups were observed interacting in the den entrance; however, these interactions were either limited to mouthing or individuals were partially obscured. Table 3 lists additional developmental landmarks observed throughout the study.

Action Patterns

Litter 1 was observed for 69.5 hours; litter 2 was observed for 60.75 hours. All behavior patterns described in previous studies (Fox 1969; Fox 1971;Bekoff, 1972; Lehner 1978; Bekoff, 1978) were documented in the present study as well. Table 4 describes the action patterns observed in the red wolves, their relative frequency and comparative data on wolves and coyotes.

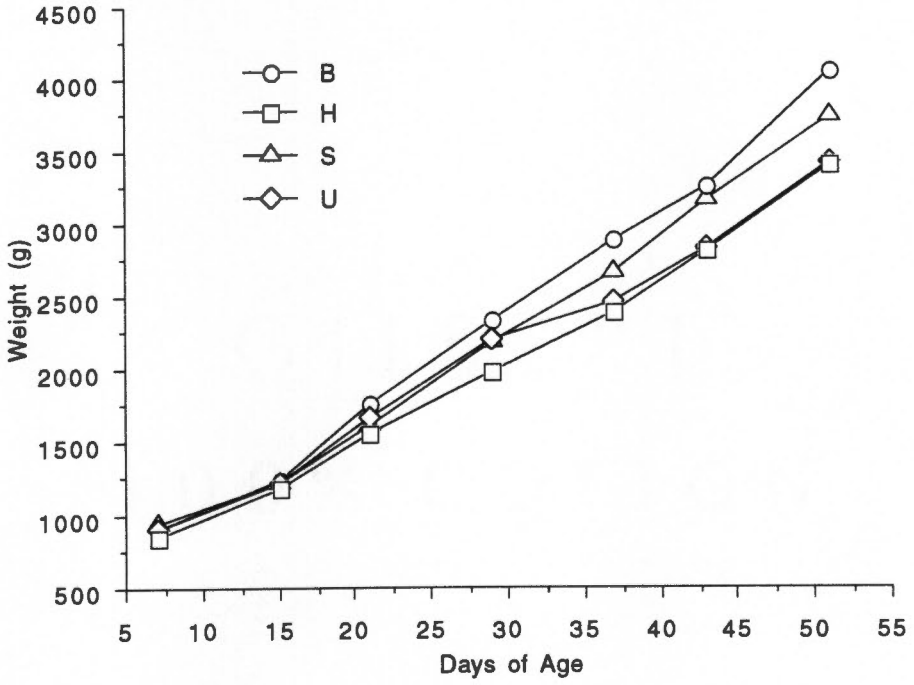

Figure 3. Individual captive red wolf pup weight changes from 7-51 days of age in Litter 2 (Knoxville)

Table 3. Median red wolf pup age (days) at first appearance of select behaviors and events

Behavior/Event	Litter	Median Age First Observed (Days)	Range (Days)	Litter	Median Age First Observed (Days)	Range (Days)
First tooth eruption	Knox	13	13-15	F Rim	-	-
Eye opening	Knox	13	12-14	F Rim	-	-
Eating solid food	Knox	31	31-33	F Rim	31	31-32
Howl	Knox	45	-	F Rim	-	-
Paw-raise	Knox	-	-	F Rim	44	-
Scrape Mark	Knox	43	-	F Rim	-	
"C" Position	Knox	47	-	F Rim	45	44-47
Object Play, Non Social	Knox	32	31-35	F Rim	33	31-34
Object Play, Social	Knox	47	43-49	F Rim	44	43-47
Unresolved Fight	Knox	32	32-34	F Rim	32	32-33
Resolved Fight	Knox	33	32-34	F Rim	33	32-33
Pup-Pup inguinal response	Knox	33	32-34	F Rim	32	32-34
Pup-pup ano-genital investigation	Knox	33	32-34	F Rim	32	32-34
Adult-pup ano-genital investigation	Knox	32	-	F Rim	36	35-38
Regurgitation	Knox	-	-	F Rim	36	
Solicitation (pup to adult)	Knox	35	35-37	F Rim	35	
Play						
Locomotor	Knox	37	36-39	F Rim	36	35-37
Wrestle	Knox	33	32-34	F Rim	32	32-33
Ambush	Knox	34	33-36	F Rim	36	35-37
Multiple actor	Knox	35	34-35	F Rim	37	36-39
Updown	Knox	36	35-37	F Rim	36	36-38
Prone	Knox	41	40-43	F Rim	44	43-45
Unreciprocated	Knox	32	31-33	F Rim	32	31-32

Table 4. Frequency of action patterns observed in captive red wolves from 28-50 days of age compared to same age wolves and coyotes. (Bekoff 1978) [1]

Red Wolf			Gray Wolf			Coyote		
Act	Total	Percent of Total Acts Observed	Act	Total	Percent of Total Acts Observed	Act	Total	Percent of Total Acts Observed
Face bite + face bite intentions	237	12.50	Chin rest	1155	15.19	Aggressive vocalization	916	11.84
General body bite	207	11.00	General body bite	881	12.34	General body bite	713	9.22
Face paw	189	9.98	Approach	571	8.00	Chin rest	700	9.05
Scruff bite + scruff bite intentions	159	8.40	Face bite + face bite intentions	544	7.62	Approach	698	9.02
Chin rest	132	6.90	Scruff bite + scruff bite intentions	502	7.03	Complete standover	500	6.46
Passive submission	123	6.50	Incomplete standover	461	6.46	Inguinal response (pup-pup)	380	4.91
Approach	123	6.00	Aggressive vocalization	419	5.87	Passive submission	351	4.53
Incomplete standover	57	3.00	Headshake	319	4.97	Face bite + face bite intentions	323	4.17
Headshake	51	3.00	Complete standover	214	2.99	Defensive vocalization	317	4.09
Play bow	25	2.38	Face paw	158	2.22	Incomplete standover	314	4.06
Aggressive vocalization	10	2.00	Defensive vocalization	146	2.04	Scruff bite + scruff bite intentions	237	3.06
Complete standover	21	1.00	Play bow	146	2.04	Headshake	237	3.06
Hip slam	21	1.00	Hip slam	123	1.72	Play bow	196	2.53
Inguinal response (pup-pup)	18	0.95	Inguinal response (pup-pup)	55	0.77	Defensive gape	187	2.41
Contactual circle	20	0.90	Contactual circle	50	0.70	Face paw	61	0.79
Defensive gape	9	0.48	Face lick	41	0.57	Hip slam	28	0.36
Defensive vocalization	6	0.32	Leap leap	36	0.50	Face lick	27	0.34
Leap leap	6	0.32	Passive submission	3	0.04	Contactual circle	16	0.2
Face lick	3	0.16	Defensive gape	2	0.02	Leap leap	0	0
TOTAL	1417	76.79	TOTAL	5826	81.09	TOTAL	6201	80.10

[1] Behaviors are arranged in descending order by percent of total acts observed for each species; red wolf pups observed from days 29-50 only, coyotes and gray wolves observed from days 21-50.

The ano-genital investigation behavior was observed. The leap leap behavior was observed in both red wolf litters (n=4 individuals total) and was most often used as a play solicitor rather than as a distinct action pattern during play. The inguinal response behavior (a slight outward rotation of a hindleg to either physical stimulation or during an agonistic encounter (Table A-1; Bekoff, 1972; Bekoff 1974a; Fox, 1971)), was observed infrequently in both litters, and rarely observed outside of direct investigation of the ano-genital region by an adult or another pup. The majority of inguinal responses observed outside of direct ano-genital investigation occurred following direct physical contact (rubbing against another pup's body or an object). The defensive gape (ears folded back against the head coupled with retraction of the lips to expose the teeth, Table A-1; Fox, 1970) was also observed. Jaw wrestling was observed frequently as pups aged and was seen as both a predominant play activity as well as during ritualized fighting.

Play and Agonistic Behavior

Play

Playful actions and play were observed from the beginning of observations in both litters. Social play was distinguished from more general affiliative actions by the use of reciprocal play markers as previously described (Table A-1, Bekoff 1972; Bekoff, 1974b). Initially, playful actions took the form of unreciprocated play in both litters (Figures 4 and 5). At 29-35 days of age, the majority of play solicits were either ignored or rebuffed by the potential partner. In litter 1, unreciprocated play decreased in frequency from days 29-35 as reciprocal play increased during the same time frame. In litter 2, unreciprocated play increased from days 29-35 to days 36-42 and was exhibited at a higher frequency than reciprocal play for the same time periods.

Play solicitors were used to initiate reciprocal play 64.3% of the time in Litter 1 (n=84) and 59.7% of the time in Litter 2 (n=186). In both litters, the most frequently used play solicitor in successful bouts was the leap behavior (Litter 1, n=15; Litter 2, n=33). The frequency of playful acts (play + unreciprocated play acts/total social acts) did not vary significantly over the developmental period observed in litter 1 (χ^2=.40, d.f.=2, p=.82) and playful acts increased from days 29-35 to days 36-42, then leveled off by days 43-50 (Figure 6). The frequency of playful acts (play + unreciprocated play acts/total social acts)varied significantly over the developmental period observed in litter 2 (χ2=6.125, d.f.=2, p=.04) and playful acts increased steadily from days 29-35 through days 43-50 (Figure 7). The percentage of time spent in play

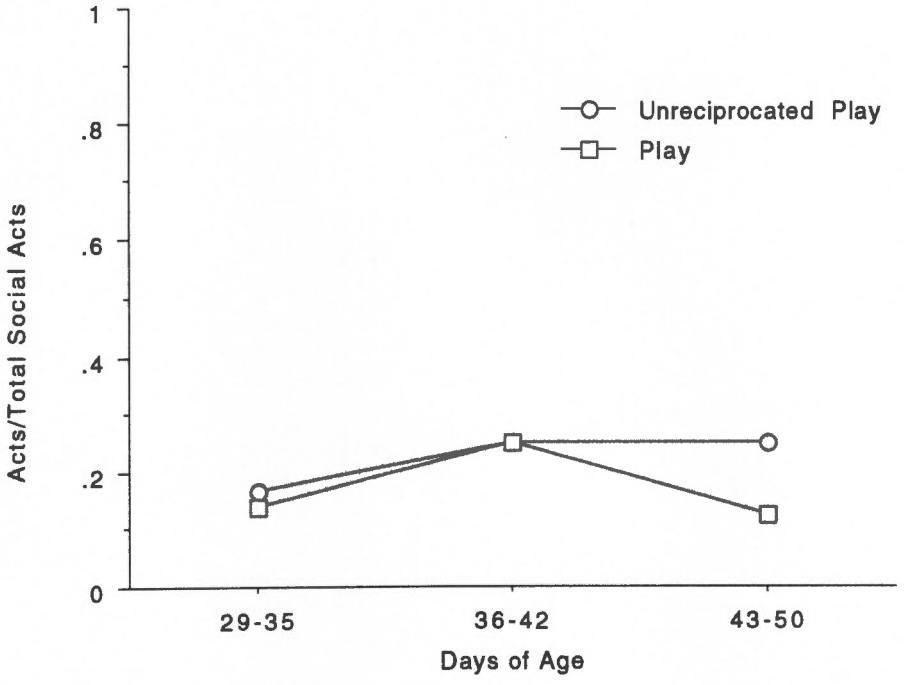

Figure 4. The median proportion of unreciprocated and social play in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

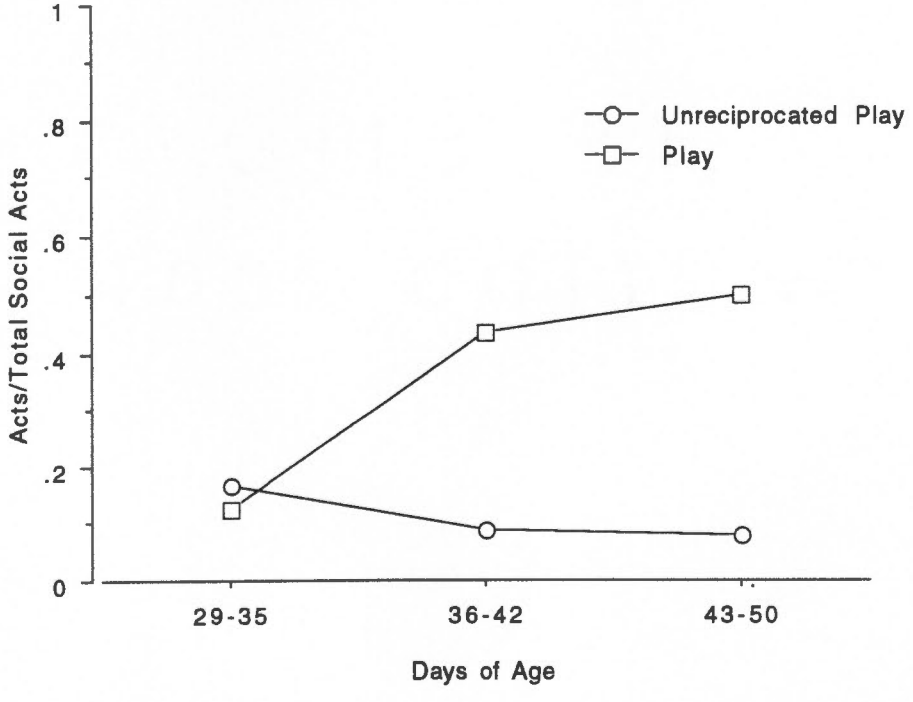

Figure 5. The median proportion of unreciprocated and social play acts in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

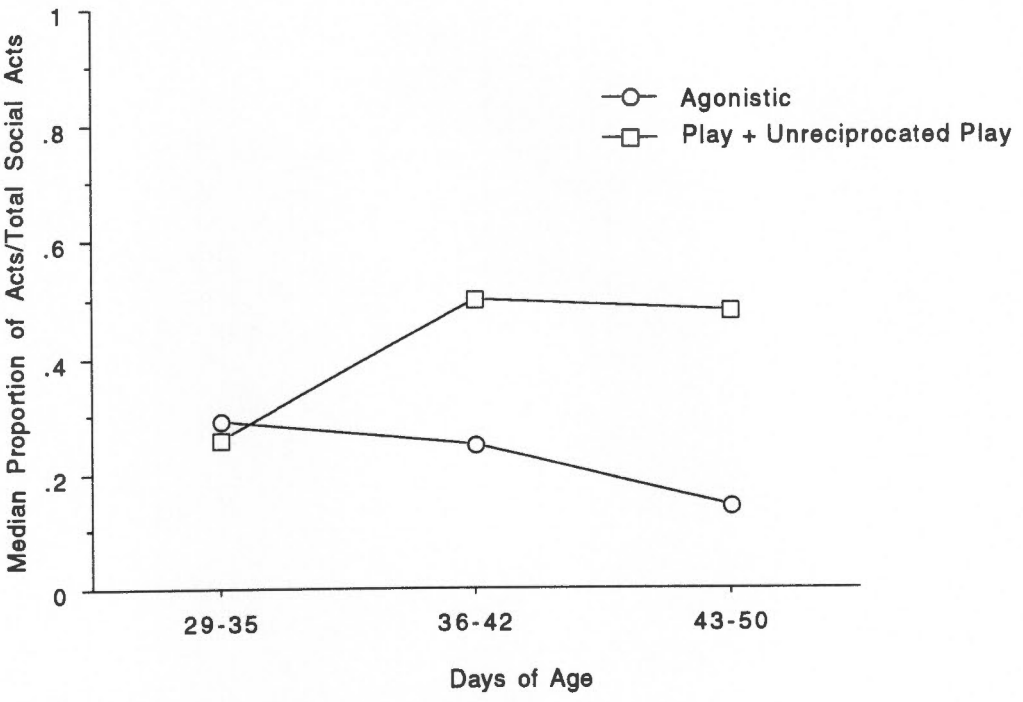

Figure 6. The median proportion of agonistic and playful acts in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

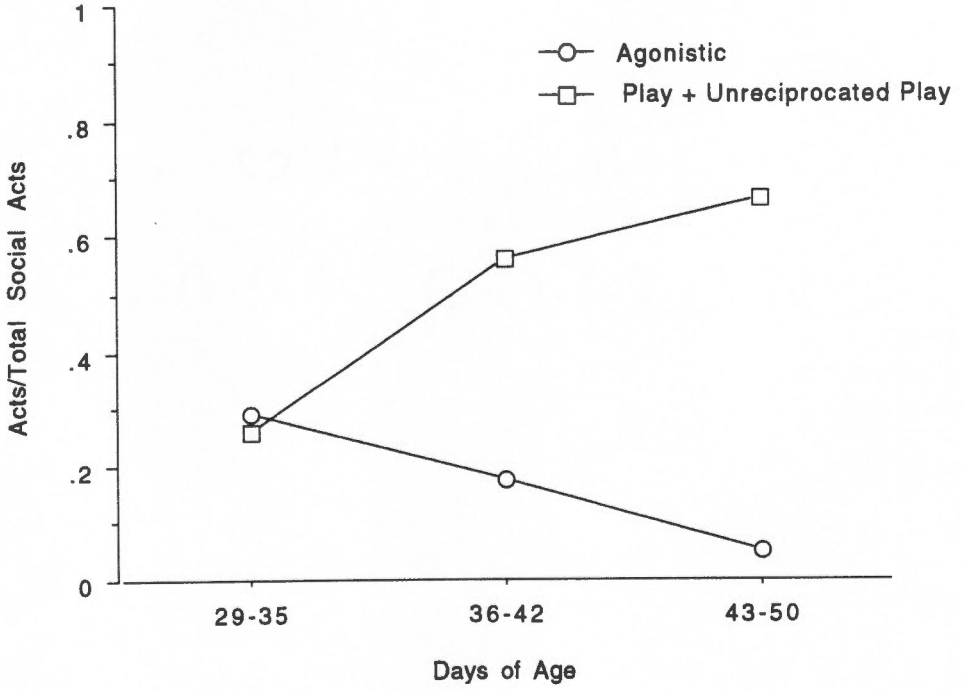

Figure 7. The median proportion of playful and agonistic acts in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

also increased from days 29-35 to days 36-42 and then leveled off in litter 1 (Figure 8). Similarly, the percentage of time spent in play increased from days 29-35 to days 36-42 and then leveled off in litter 2 (Figure 9).

The type of play observed changed over time (Table 2, Figures 10 and 11). In both litters, locomotor and wrestle play were the predominant play types initially; multiple actor, ambush, updown and prone play did not appear until day 36 and later. Additionally, in both litters, prone play was the last play type to develop.

Within both litters, individual differences in playfulness were not observed: there were no significant differences in the frequency of unreciprocated (Litter 1 H=4.207, d.f.=4, p=..37; Litter 2 H=1.57, d.f.=3, p=.67) or reciprocal play acts performed across pups during the time periods observed (Litter 1 H=4.6, d.f.=4, p=.33; Litter 2 H=.682, d.f.=3, p=.88). Between litters, there were no significant differences in the proportion of unreciprocated play acts exhibited over time (Z=1.44, p=.15); however, litter 2 was significantly more playful (proportion of play acts/total social acts) than litter 1 (Z=2.544, p=.01) (Figure 12). There were no sex differences noted across litters in the proportion of unreciprocated or reciprocal play acts, play-soliciting or the duration of time spent in play (Z=-.05, p=.95; Z=-.58, p=.56; Z=-.34, p=.73; and Z=-.68, p=.49 respectively).

Agonism

Agonistic interactions were first observed at the beginning of the observation period in both litters (Figures 6 and 7). Initial agonistic interactions were primarily in the form of standovers and were distinguished from neutral or playful interactions by the use of aggressive and/or defensive vocalizations, erect postures and agonistic facial expressions. Unresolved fights (no clear "loser"observed by the subject's use of passive submissive behaviors, distress vocalizations or retreat) began on day 32 (litters 1 and 2). Fights began to be resolved shortly thereafter in both litters on day 33. However, relatively few total fights were observed (Litter 1 n=84, Litter 2 n=42) and agonistic interactions took the form of threats in most cases.

The frequency of agonistic interactions (as a proportion of all social interactions) did not vary significantly over the developmental period in litter 1 (χ^2=1.6, d.f.=2, p=.49). The frequency of agonistic interactions did vary significantly over the developmental period observed in litter 2 (χ2=8.0, d.f.=2, p=.02). In the latter case, the proportion of agonistic acts decreased steadily from days 29-35 through days 43-50 (Figure

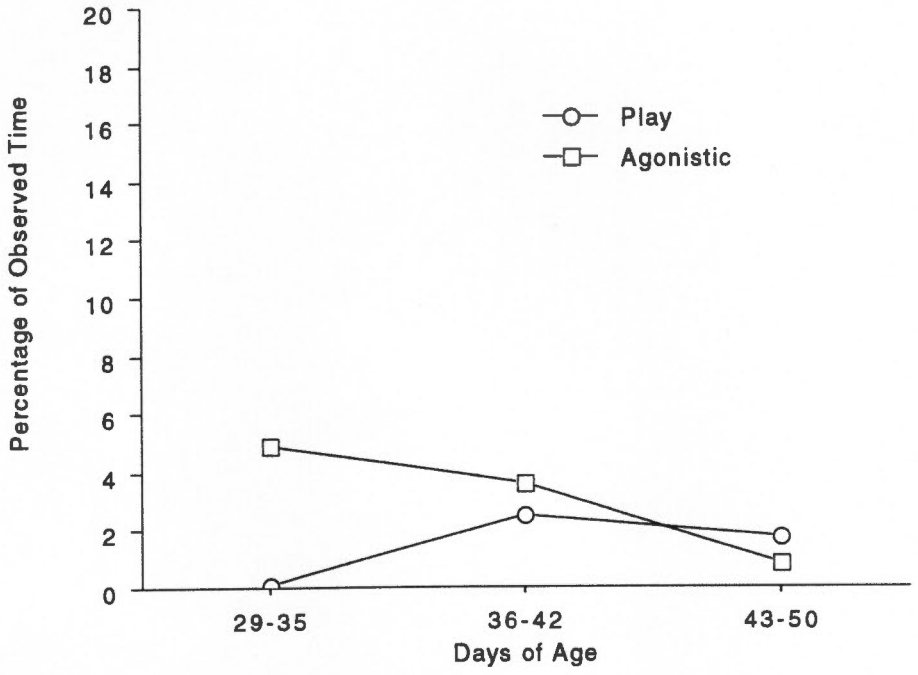

Figure 8. The median percentage of observed time in play and agonistic interactions in captive red wolves from Litters 1 (Fossil Rim) at three different time periods (4 -6 weeks of age)

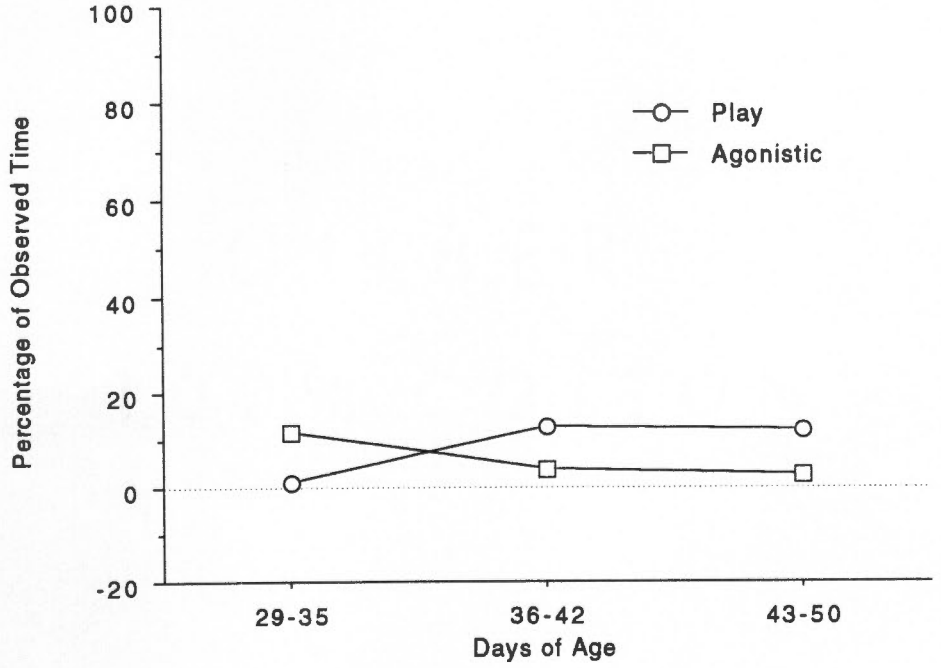

Figure 9. The median percentage of observed time in play and agonistic interactions in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

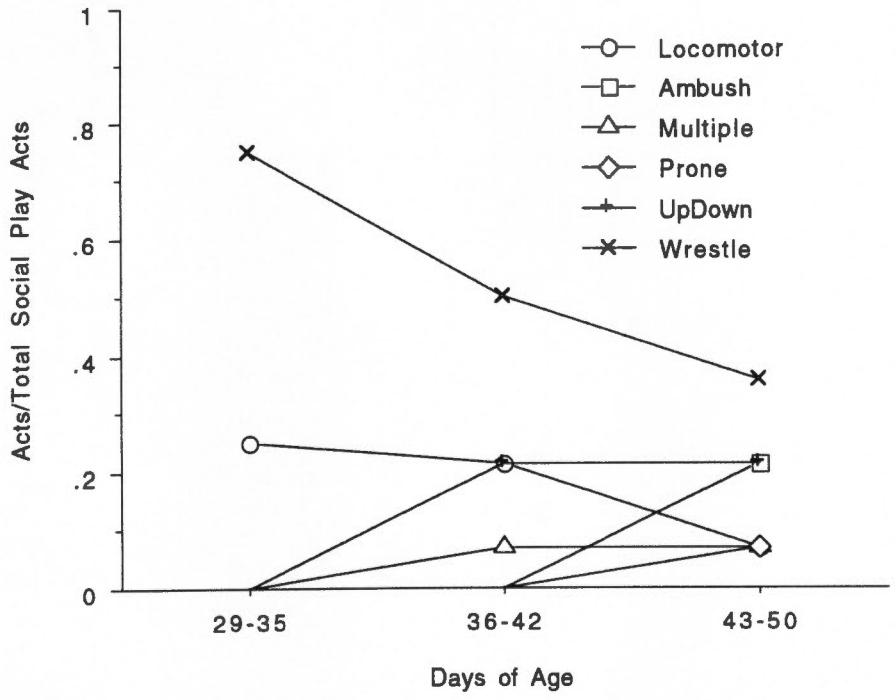

Figure 10. The median proportion of play types in captive red wolves from Litter 1 (Fossil Rim at three different time periods (4-6 weeks of age)

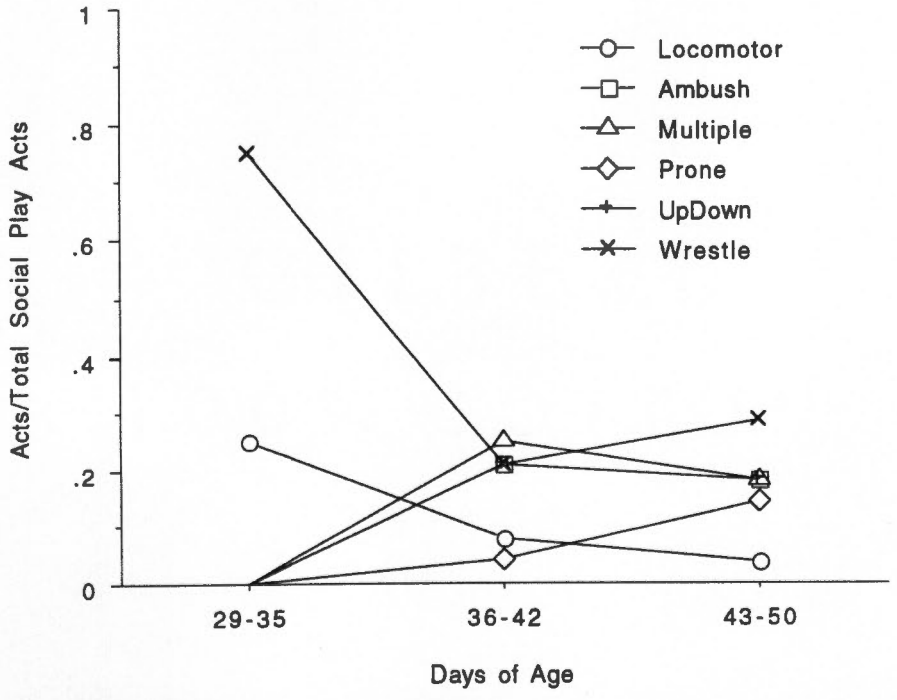

Figure 11. The median proportion of play types in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

7). While the proportion of agonistic interactions decreased over time in litter 1, the rate of decline was not as dramatic as that in litter 2 where agonistic interactions were rarely observed in days 43-50.

Quantitative individual pup differences in agonistic behavior were not observed; there were no significant differences in the proportion of agonistic acts performed across pups (Litter 1 H=8.5, d.f.=4, p=.08; Litter 2 H=1.95, d.f.=3, p=.58). However, there were litter differences in the proportion of agonistic behaviors; litter 1 was significantly more agonistic than litter 2 (Z=2.102, p=.03) (Figure 13). Sex differences were not observed across litters in the proportion of aggressive acts or the duration of time spent in aggressive acts (Z=-.94, p=.35; Z=-.956, p=.34 respectively).

Play and Agonistic Behavior Compared

In both litters, agonistic interactions were more frequent than all other pup-pup interactions early in development (days 29-35) as measured by both the proportion of social interactions that were agonistic as well as the percentage of observed time (Figures 6, 7, 8 and 9). The proportion of reciprocal social play increased only after the proportion of agonistic behaviors had decreased (though the decrease in litter 1 was less dramatic than that in litter 2). Furthermore, during the same developmental period in which the proportion of agonistic interactions remained somewhat elevated (days 43-50), play-soliciting took the form of unreciprocated play rather than reciprocal social play in both litters (Figures 4, 5, 6 and 7).

Object Play

Object play was first observed early in development in both litters (Table 2) and peaked in frequency (as a proportion of total social acts) in litter 1 during days 43-50 and in litter 2 during days 36-42 (Figures 14 and 15). There was no significant difference between time periods in the proportion of object play acts observed (object play acts/total social acts) in either litter (litter 1 χ^2=.4, d.f.=2, p=.81; litter 2 χ^2=.5, d.f.=2, p=.78). In both litters, the proportion of object play (object play/total social acts) increased concurrently with the increase in the proportion of playful pup-pup interactions and the decrease in the proportion of agonistic interactions.

The form of object play bouts changed over time. Initially (days 29-42), object play bouts in both litters were primarily non social bouts (pup-object) as opposed to social object play bouts (pup-pup-object). Object play changed to a combination of both non social and social object play bouts during days 43-50

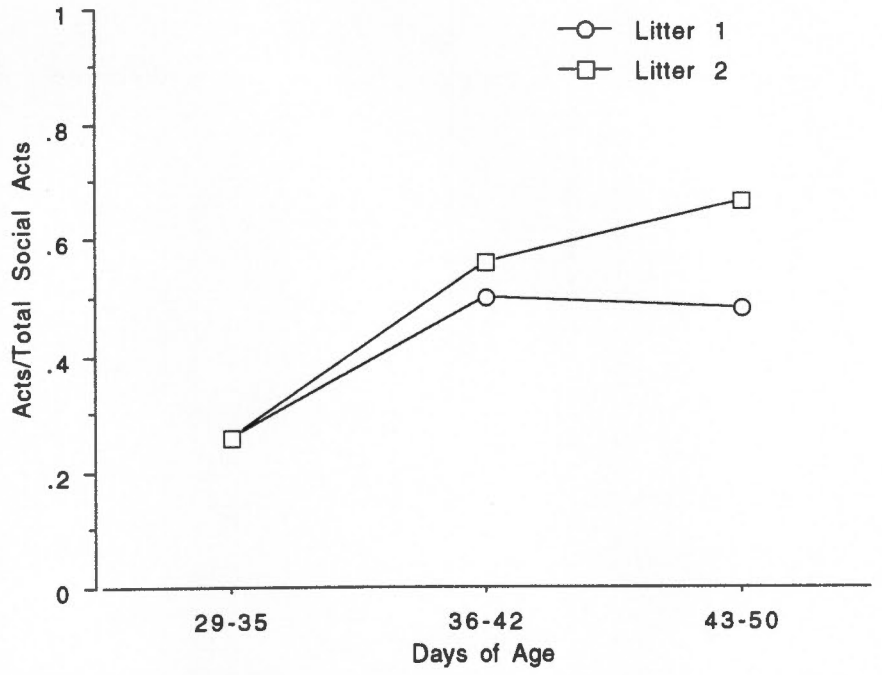

Figure 12. The median proportion of playful acts in captive red wolves from Litters 1 (Fossil Rim) and 2 (Knoxville Zoo) at three different time periods

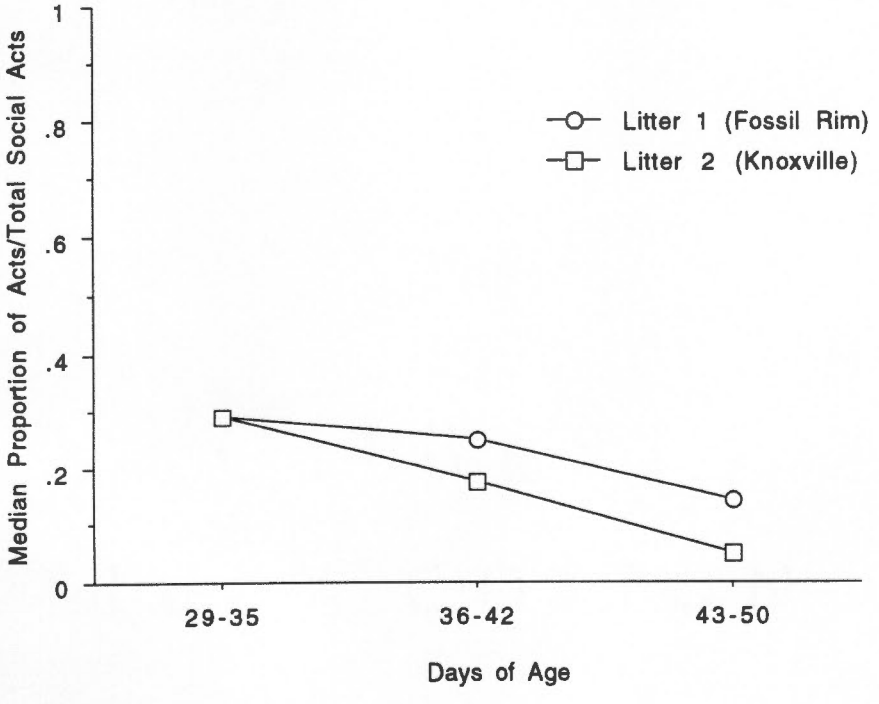

Figure 13. The median proportion of agonistic acts in captive red wolves from Litters 1 (Fossil Rim) and 2 (Knoxville Zoo) at three different time periods (4 -6 weeks of age)

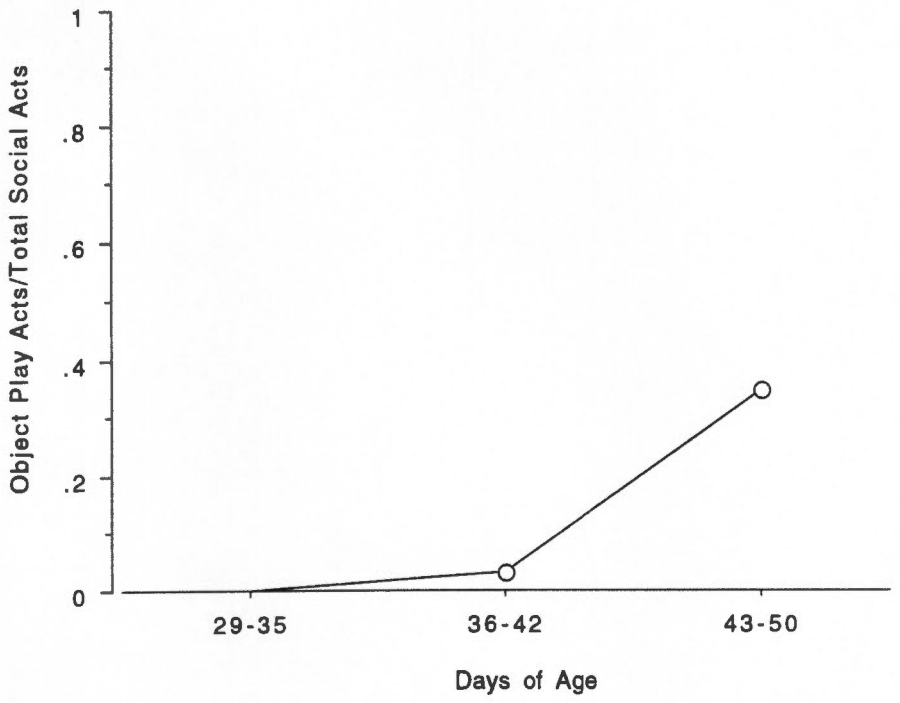

Figure 14. The median proportion of object play acts compared to all social acts in captive red wolves from Litter 1 at three different time periods (4 -6 weeks of age)

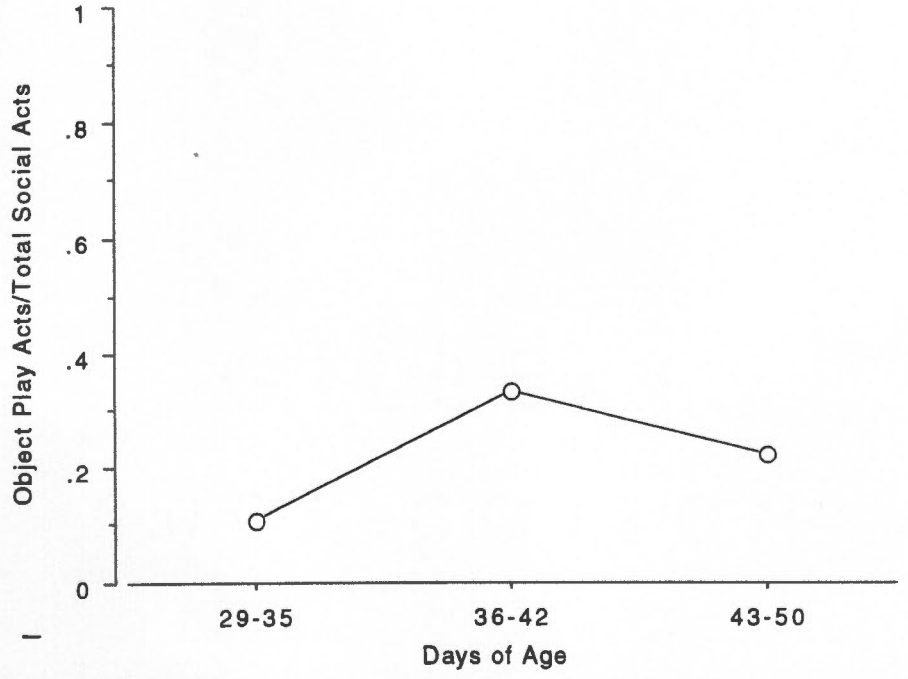

Figure 15. The median proportion of object play acts compared to all social acts in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

(Figures 16 and 17) (concurrent with the increase in reciprocal social play and the decrease in agonistic behavior in both litters, Figures 6 and 7).

There were no significant differences in the proportion of object play bouts (object play/ total social interactions) across individual pups in either litter (litter 1 H=3.78, d.f.=4, p=.44; litter 2 H=2.24, d.f.=3, p=..53). There were also no significant sex differences noted across litters in the proportion of object play bouts or in the proportion of non social or social object play bouts (Z=-.14, p=.89; Z=-.77, p=.44; Z=-.59, p=.55 respectively.) However, the two litters did differ significantly in the proportion of total object play (as a proportion of all social interactions) over time (Z=2.544, p=.01) and in non social object play (as a proportion of all object play bouts) (Z=2.764, p=.005).

Adult-Pup Interactions

In both litters, pups spent significantly more time in proximity to the female throughout the entire study period (Litter 1: Z=-2.067, p=.04; Litter 2: Z=-2.824, p=.004). However, proximity to each adult changed over time in both litters (Figures 18 and 19). Initially (days 29-35), pups spent more time in proximity to the female than the male. By days 43-50, however, the amount of time the pups spent in proximity to the female alone decreased, while time spent in proximity to the male as well as both the female and the male increased. These trends were not statistically significant (litter 1: proximity to adult female χ^2=2.8, d.f.=2, p=.25; proximity to adult male χ^2=2.8, d.f.=2, p=.25; proximity to both adult male and female χ^2=.4, d.f.=2, p=.82 and litter 2: proximity to adult female χ^2=.5, d.f.=3, p=.78; proximity to adult male χ^2=1.5, d.f.=2, p=.47; proximity to both adult male and female χ^2=.13, d.f.=2, p=.94).

Adult-pup interactions took the form of disciplinary (involving at least one full or inhibited adult-pup directed bite), investigative (ano-genital investigation or sniffing) or affiliative interactions (play-soliciting, pup-adult directed general body bites, muzzle-muzzle contact, face-licking). The frequency and form of these interactions varied by litter. Similarly, the individual involved (adult male or female) differed between litters.

While adult-pup interactions were observed less frequently in litter 1 compared to litter 2, male-pup interactions were more frequently observed than female-pup interactions in both litters (Figures 20 and 21): in litter 1, adult-pup interactions were predominantly male-pup interactions across all time periods; in litter 2

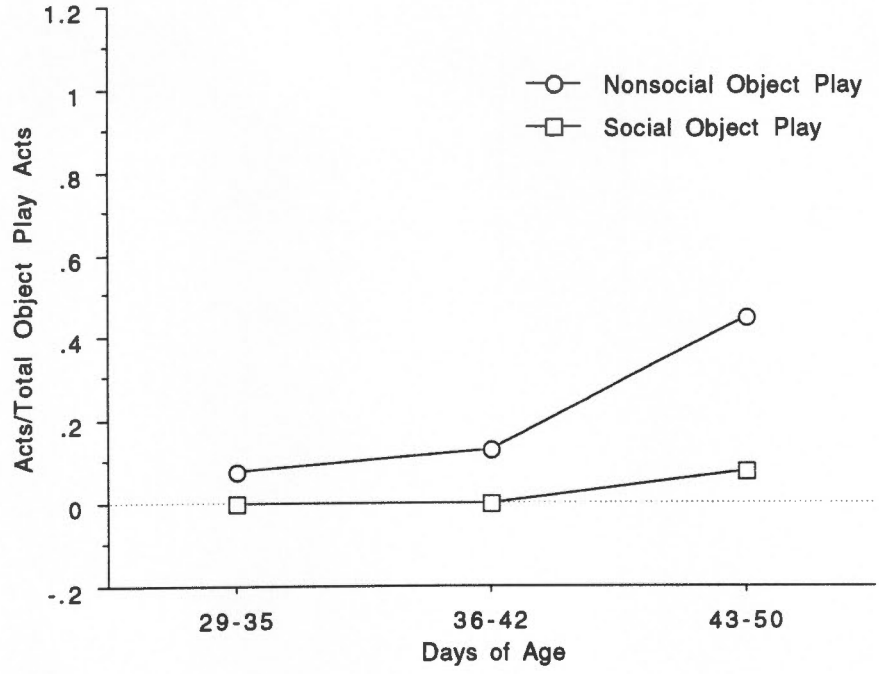

Figure16. Changes over time in the median proportion of non social and social object play acts in Litter 1

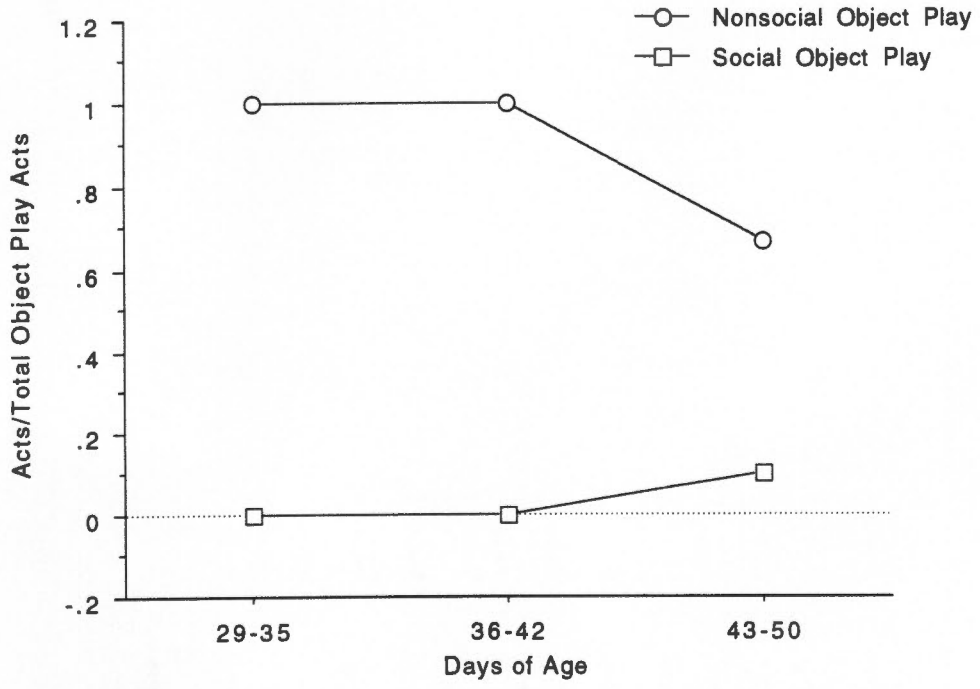

Figure 17. The median proportion of non social and social object play acts in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

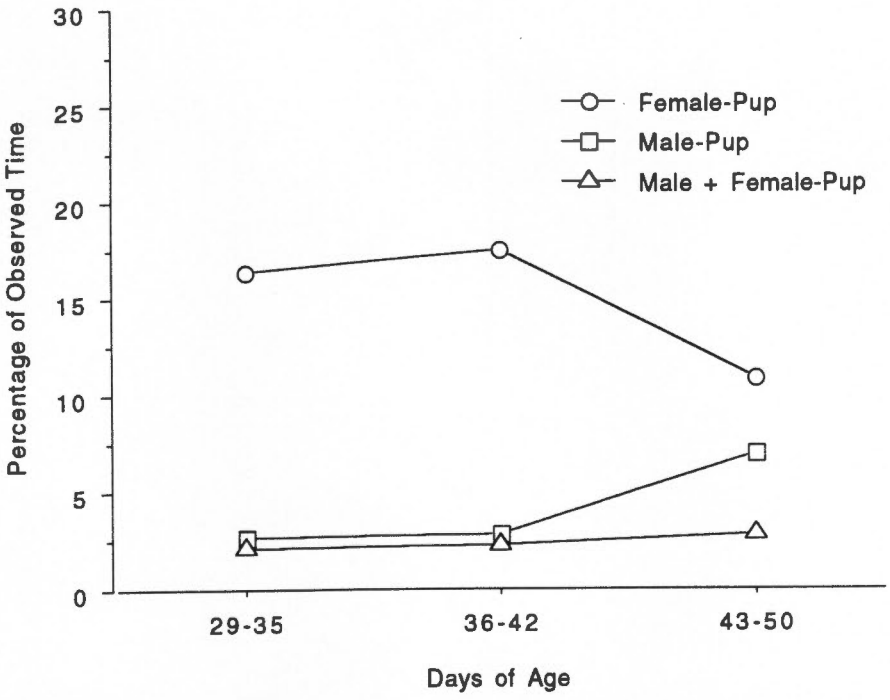

Figure 18. Adult-pup proximity (expressed as median percentage of time that pups were in proximity to either the adult male, female or both)in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

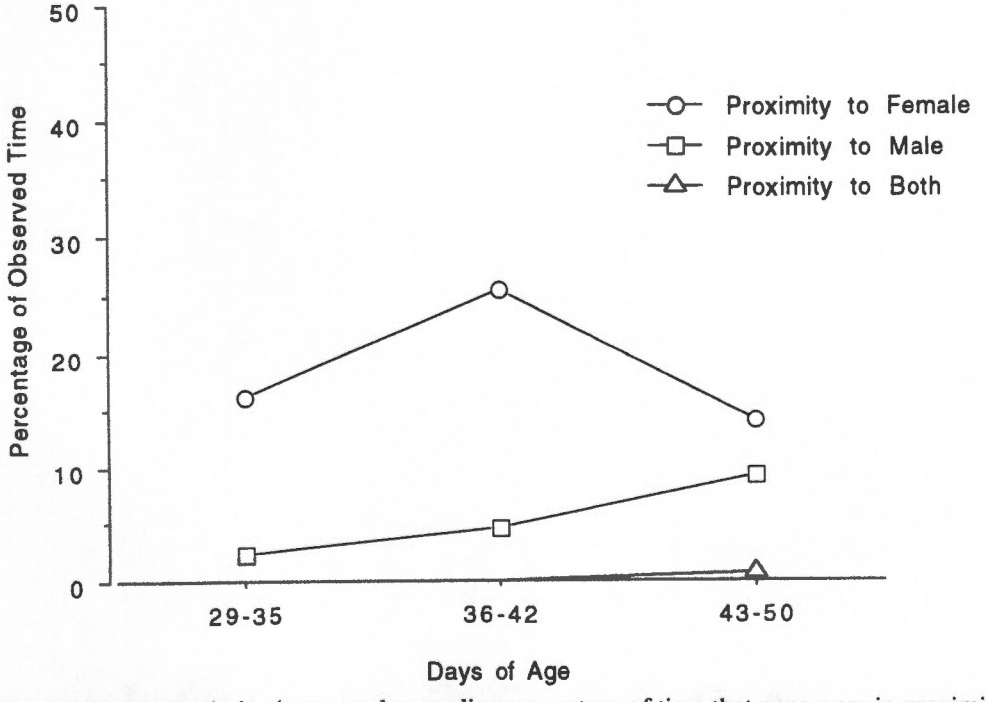

Figure 19. Adult-pup proximity (expressed as median percentage of time that pups were in proximity to either the adult male, female or both) in captive red wolves from Litter 2 (Knoxville) at three different time periods (4-6 weeks of age)

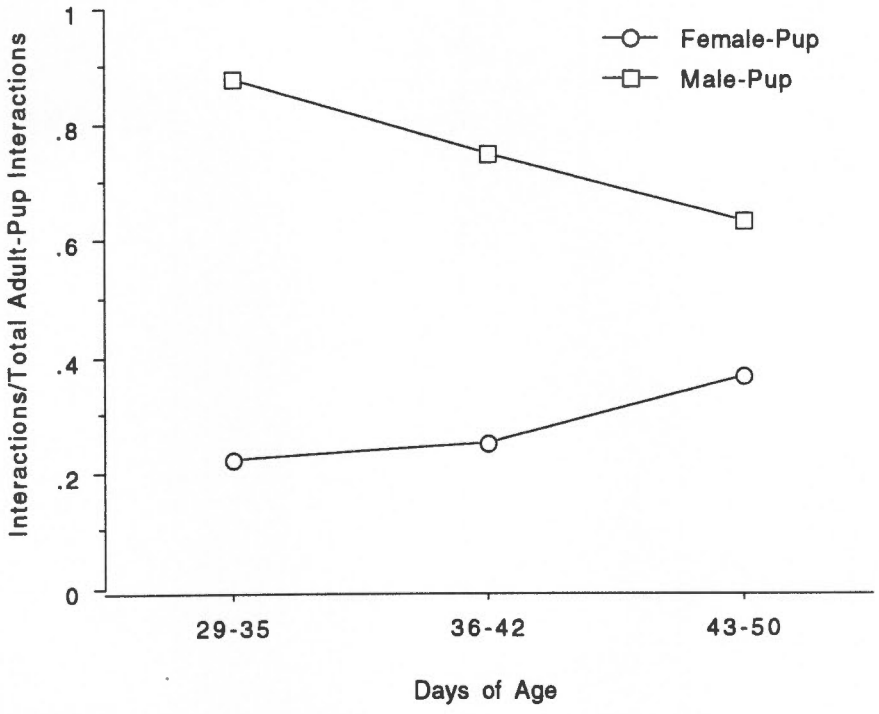

Figure 20. The distribution of adult-pup interactions by adult sex in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

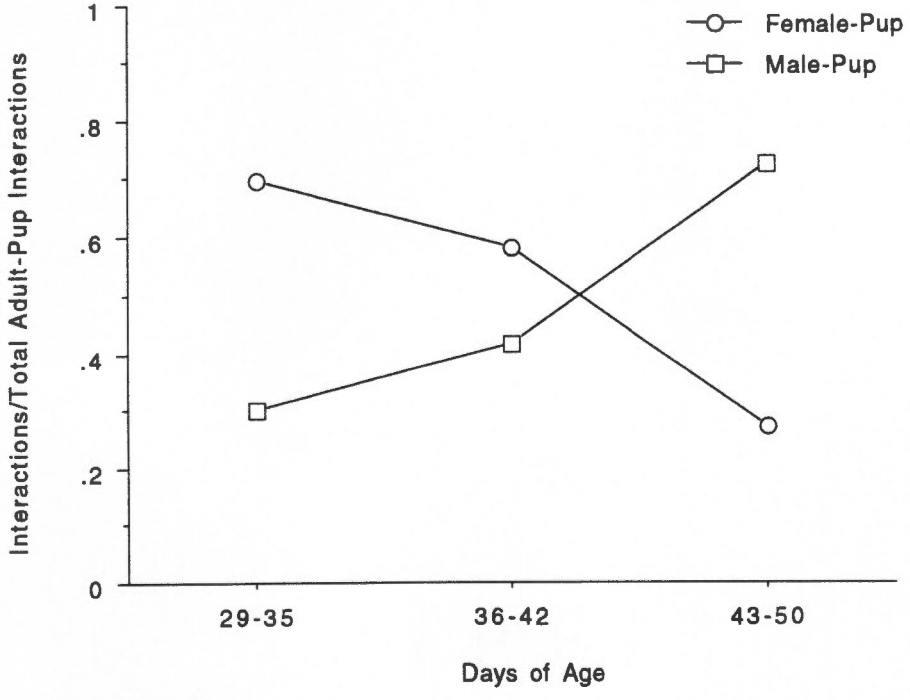

Figure 21. The distribution of adult-pup interactions by adult sex in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

male-pup interactions only occurred at a higher frequency (interactions/total adult-pup interactions) than female-pup interactions during days 43-50. Pup discipline was performed by the adult-male in both litters: of all interactions including at least one bite (full or inhibited) directed towards a focal pup, significantly more were performed by the adult male than the female in both litters (litter 1: $Z=-1.604$, $p=.10$; litter 2: $Z=-2.089$, $p=.04$; Figures 22 and 23 respectively). In litter 1, agonistic interactions between parents and young occurred to the almost total exclusion of investigative or affiliative interactions. Investigative interactions that were observed in litter 1 were performed by the adult male (Figure 24). Conversely, ano-genital investigations were observed frequently in litter 2 and were performed by both adults (Figure 25). Very few affiliative adult-pup interactions were observed in litter 1 (Figure 26); however, the male in litter 2 actively solicited play from and played with pups (Figure 27). Female affiliative interactions in litter 2 were primarily muzzle-muzzle contacts and face-licks.

No significant adult-pup preferences were noted in either litter in the duration of adult-pup proximities or the proportion of adult-pup interactions. Similarly, no adult-pup preferences were noted by sex of the pup in adult-pup proximities, the proportion of total interactions or in the proportion of ano-genital investigations, disciplinary bites or affiliative actions (Male-pup: $Z=-.70$, $p=.48$; $Z=-1.23$, $p=.20$; $Z=-1.04$, $p=.29$; $Z=-.749$, $p=.45$; $Z=-.23$, $p=.81$ respectively; Female-pup: $Z=-.69$, $p=.49$; $Z=-1.23$, $p=.21$; $Z=-.25$, $p=.80$; $Z=-.16$, $p=.87$; $Z=-.06$, $p=.95$ respectively).

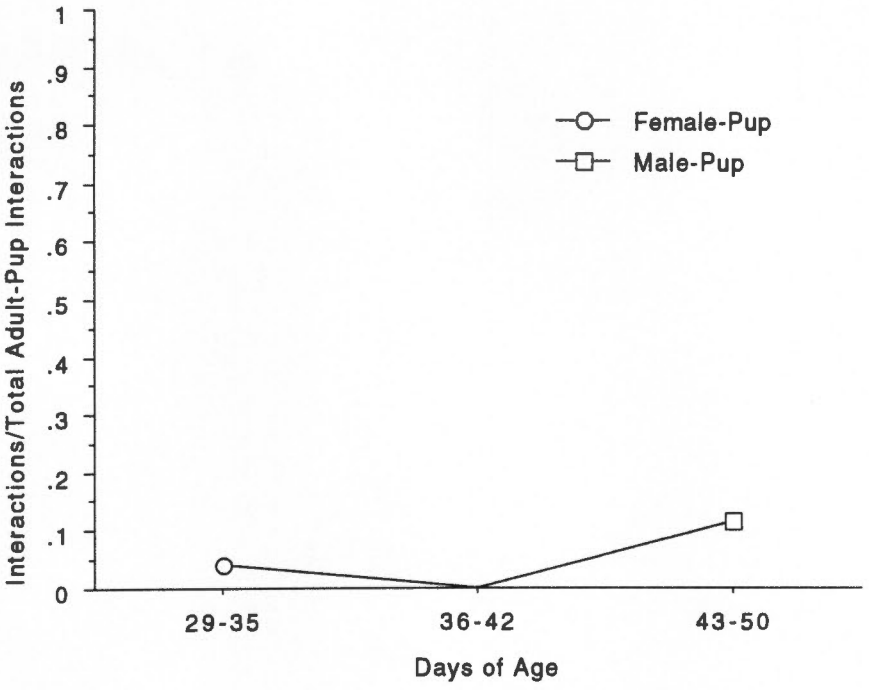

Figure 22. The median proportion of adult-pup interactions that included a"disciplinary" bite in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

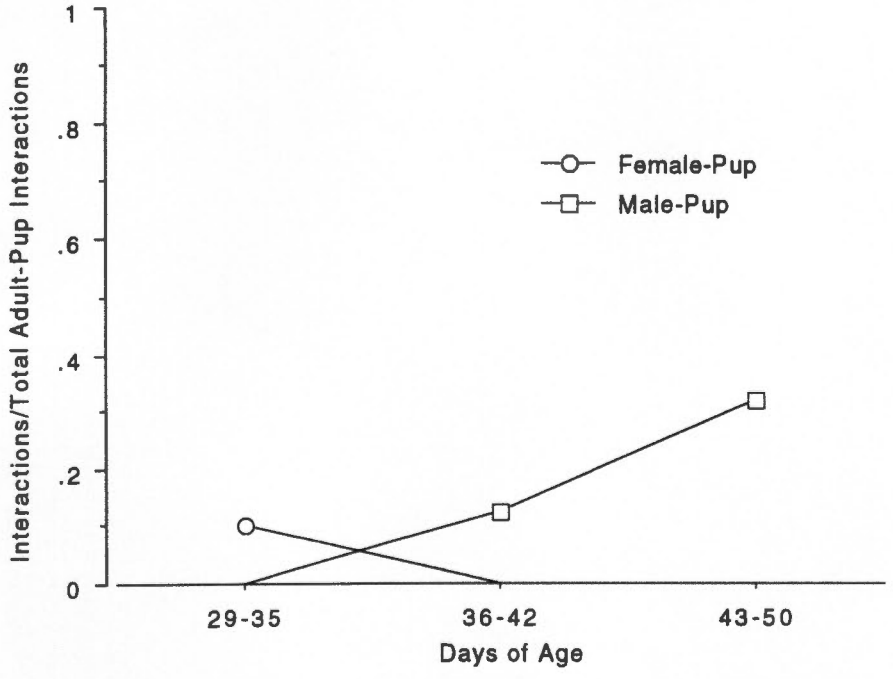

Figure 23. The median proportion of adult-pup interactions that included a"disciplinary" bite in captive red wolves from Litter 2 (Knxoville) at three different time periods (4-6 weeks of age)

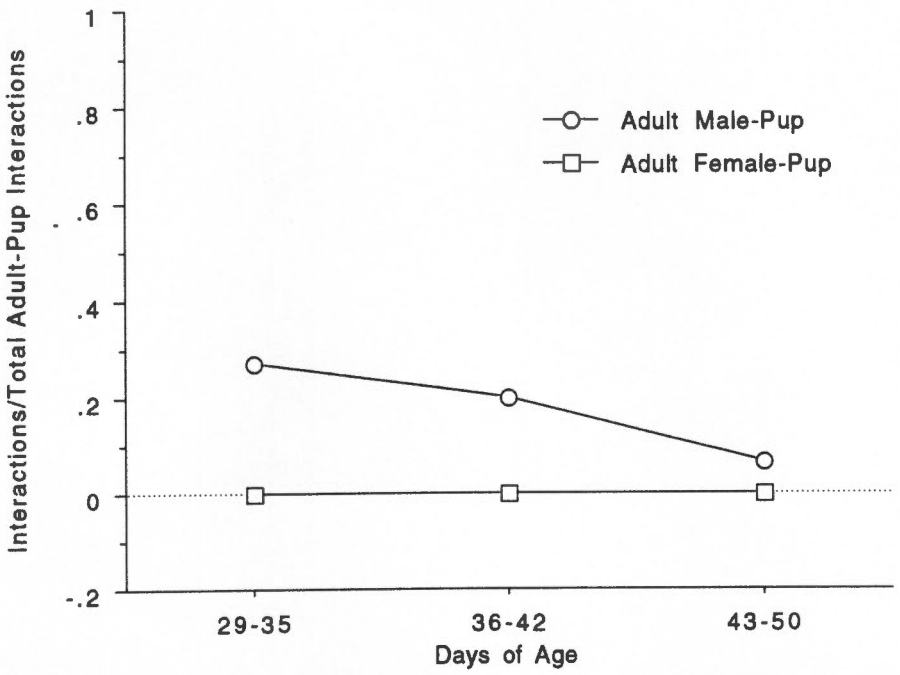

Figure 24. The median proportion of adult-pup acts that included an ano-genital investigation in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

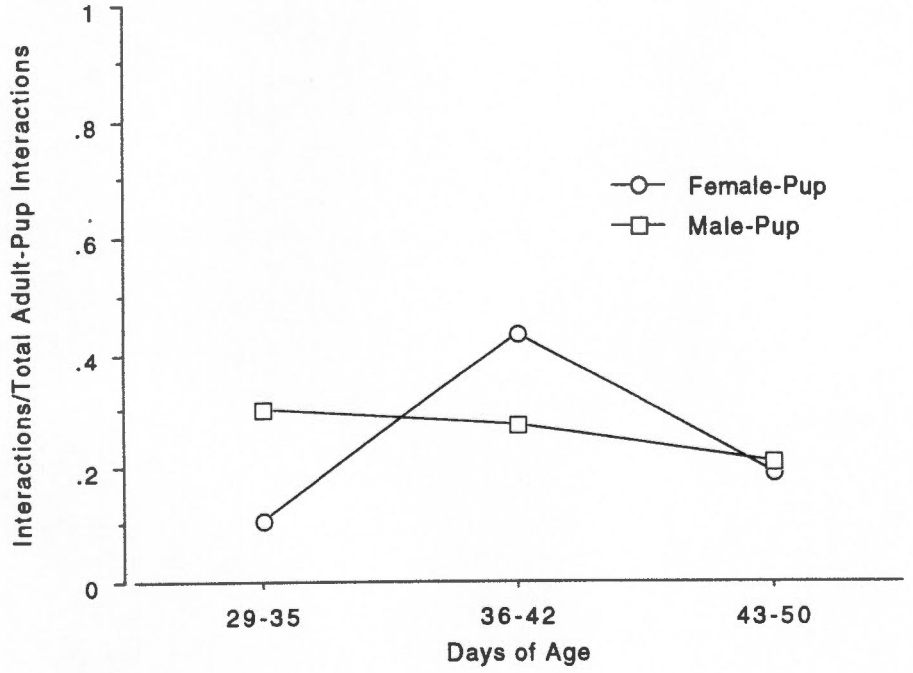

Figure 25. The median proportion of adult-pup acts that included an ano-genital investigation in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

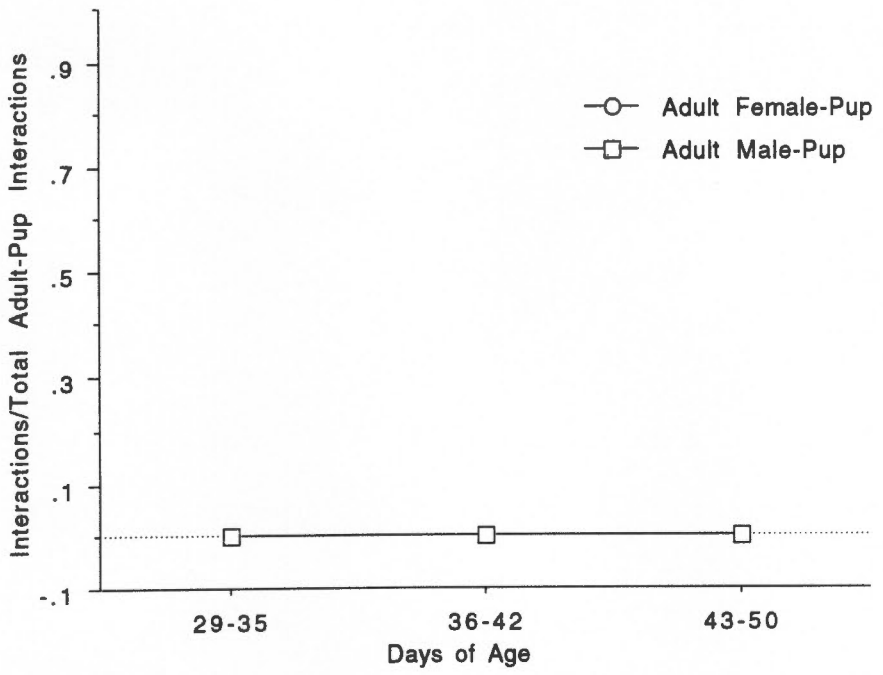

Figure 26. The median proportion of adult-pup affiliative interactions in captive red wolves from Litter 1 (Fossil Rim) at three different time periods (4-6 weeks of age)

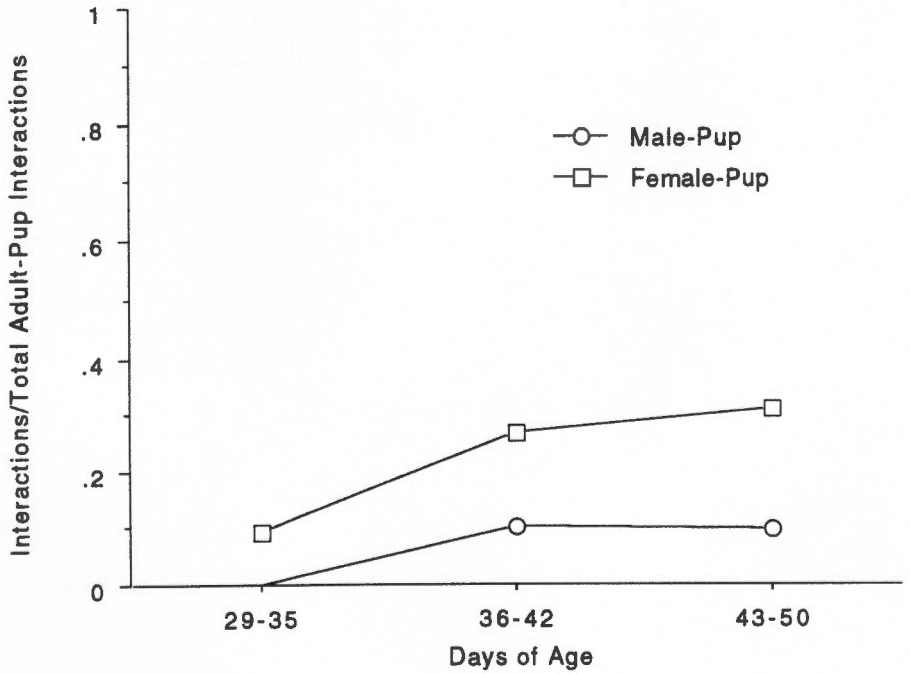

Figure 27. The median proportion of adult-pup affiliative interactions in captive red wolves from Litter 2 (Knoxville Zoo) at three different time periods (4-6 weeks of age)

Chapter 4
Discussion

This study has quantified numerous factors related to the previously unknown patterns of red wolf socialization and ontogeny of early behavior. Table 5 and Figure 28 outlines these findings and compares these data to that previously documented in coyotes and wolves.

Physical and Early Development

Physical development data were obtained from one litter (n=4 individuals). The mean developmental age at eye opening is similar to that reported for coyotes and wolves while the order of tooth eruption differed (Table 5; Bekoff & Jamieson 1975). In the case of the red wolves, lower canines erupted before upper incisors while the two erupted concurrently (on average) in the coyotes. Red wolf teeth erupted on average later than that reported in coyotes (Bekoff & Jamieson 1975; Bekoff 1978). Delayed tooth eruption has also been reported in the eastern coyote (Bekoff 1978) and the domestic dog (Scott & Fuller 1965; Bekoff & Jamieson 1975). It has been hypothesized in both cases that the delayed tooth eruption is related to mixed ancestry. Red wolf birth weights were not available; however, throughout development the litter of red wolves was much heavier than that reported for coyotes, yet less than that reported for wolves (e.g. day 30, coyotes=867g, day 30, gray wolves= 4,500 g. day 29, red wolves=2172 g (Bekoff, 1978; Bekoff & Jamieson 1975; Mech 1970)).

Age at first emergence from the den was similar to that reported for both coyotes and wolves (Table 5; Bekoff 1978; Mech 1970). Pups began eating solid food shortly after emerging from the den. In some cases, actual consumption of food was difficult to determine since pups were seen mouthing food upon first encountering it. Two howls were noted during the study (both Litter 2), and the time course in development was similar to that reported for both coyotes and wolves (Table 5). Two behaviors bear mentioning since they have not previously been recorded in either wolf or coyote pups so young. A pup in litter 2 was observed to scrape-mark following defecation on day 43. Despite numerous defecations recorded by other pups (in both litters), this behavior was only observed in the single individual. Simpson (1975) first observed scrape marking in coyotes much later, at 23 weeks of age. A pup in litter 1 was observed to "paw-raise" while investigating an unidentified scent on day 44; however, this behavior was only observed one time.

Table 5. Patterns of physical and behavioral development in gray wolves, red wolves and coyotes

Behavior	Gray Wolf	Red Wolf [1]	Coyote
Physical Development			
Eye-opening	11-14 days[2]	12-14 days, avg. 13 days	avg. 14 days [3]
Weight at 30 days of age	4,500 g [2]	2172 g (day 29)	867 g [3]
Tooth eruption order	few front teeth on day 15 [2]	upper canine (day 13), lower canine (16), upper (19.5) and lower incisor (19.5)	upper canines (day 14), lower canines and upper incisors (14-15), and lower incisors (16) [3,4]
Age at emergence from den	27 [2]	28; 27 (litter 1; 2)	28 [3,4]
Parental Behavior			
Female-pup	Little disciplinary behavior noted towards pups [2]	Little disciplinary behavior noted towards pups	Little disciplining by female until 33 days of age [4]
	No apparent nursing order [2]	No apparent nursing order	No nursing order [4]
	No preferential treatment towards any pup by the female [2]	No preferential treatment towards any pup by the female	No preferential treatment towards any pup by the female [4]
	All pack members, especially the alpha female, investigate the pups through muzzle-fur contact [7]	Female initiated the majority of interactions with pups. Interactions were predominantly investigative.	Female never initiated interaction (aggressive or playful) with any of the pups [4]
		Female never interfered with a pup-pup interaction, but did seek out and attend to pups following aggression	Female never interfered with a pup-pup interaction [4]
Male-pup		Significant male-pup aggression in one of two litters	Significant male-pup aggression [4]
		Male routinely vocalized to pups in den	
	Low ranking males play with juveniles, seldom with pups [7]	Male solicited play and interaction with pups in litter [2]	

Table 5. (continued).

Behavior	Gray Wolf	Red Wolf [1]	Coyote
General	Playful parent-young interactions common [6]	Playful parent-young interactions common	Very few playful parent-young interactions observed [4]
Behavioral Repertoire			
Form of behaviors observed	See Bekoff 1978	Similar to that documented for coyotes and gray wolves	See Bekoff 1978
Sexual play	Frequent; can appear as early as 4 weeks of age [4,5]	None observed in course of study	Infrequent; does not appear until 14-15 weeks of age [4, 5]
Marking behavior	First observed	Single pup performed a scrape mark following defecation on day 43	First observed from 94 days-44 weeks of age (leg-lifting in males); 22-44 weeks (scrape marking) [4]
Inguinal response	Very infrequent [4,6]	Pup-pup inguinal responses observed infrequently; frequent inguinal responses to direct ano-genital stimulation from adults	Frequent; a species-specific behavior [4,6]
Leap-leap	Observed infrequently; a species-specific behavior [4,6]	Observed, but at a relatively low frequency	Never observed; not part of the species behavior repertoire [4,6]
Agonistic Behavior			
Timetable	Follows development of social play [2,4,5]	Precedes development of social play	Precedes development of social play [4,5]
Form	Ritualized threat behavior; limited severe fighting [2,4,5]	Primarily threat behavior	Severe aggression; bites uninhibited [4,5]
Passive submission	Frequent [2,4,5]	Rarely observed	Rarely observed [4,5]
Active submission	Frequent [4]	Rarely observed	Rarely observed [4]
Aggressive vocalization	Infrequent [4,5]	Rarely observed	Frequently observed; days 21-28 particularly [4,5]
Defensive gape	Rarely observed [2,4,5]	Rarely observed	Frequent [4,5]

Table 5 (continued)

Behavior	Gray Wolf	Red Wolf [1]	Coyote
Rank-related aggression	Not observed prior to 50 days of age (occurs during latter part of first year) [2,4,5]	Not observed in course of current study	Observed during 4-5 weeks of age [4,5]
Standing over	Observed in both playful and agonistic contexts [4,5]	Observed in both playful and agonistic contexts	Observed predominantly in agonistic contexts [4,5]
Social Play Behavior			
Timetable	Precedes development of agonistic behavior [2,4,5]	Follows development of agonistic behavior	Follows development of agonistic behavior [4,5]
Use of play intention signals	Precede play bouts with play intention signals 30% of the time [4]	Precede play bouts with play intention signals 64.3% and 59.7% of time (litter 1 and 2 respectively)	Precede play bouts with play intention signals 90% of the time [4,5]
Rank-related play soliciting ability	N/A; no dominance hierarchy present at this age [2,4]	N/A; no dominance hierarchy present at this age	Higher ranking individuals less successful in initiating play than lower-ranking ones [4]
Prolonged jaw wrestling	Observed frequently [2, 5]	Observed frequently	Rarely observed [5]
Sex differences	None observed [4,5]	None observed	None observed [4,5]
Dominance Hierarchy	Established later in development; post 50-days [2,4,5]	None observed	Established early in development by agonistic encounters [4,5]

Sources:

1 Wagener, 1998. The ontogeny of red wolf (*Canis rufus*) social behavior: Implications for sociality and taxonomic status. M.S. thesis. University of Tennessee, Knoxville, TN.

2 Mech, L.D. 1970. The Wolf: Ecology of an Endangered Species. New York: Natural History Press.

3 Bekoff, M., and Jamieson, R. 1975. Physical development in coyotes (*Canis latrans*), with a comparison to other canids. Journal of Mammalogy 56(3):685-692.

4 Bekoff, M. 1972. An ethological study of the development of social interaction in the genus *Canis*: A dyadic analysis. Ph.D. dissert., Washington Univ., St. Louis, Miss.

5 Bekoff, M. 1978. Behavioral development in coyotes and Eastern coyotes. In: M. Bekoff, ed. Coyotes: Biology, Behavior and Management, pp. 97-126. New York: Academic Press.

Table 5 (continued)

Sources (continued):

[6] Fentress, J.C. and J. Ryon. 1982. A long-term study of distributed pup feeding in captive wolves. Pp. 238-261 In: F.H. Harrington and P.C. Paquet eds. Wolves perspectives of behavior, ecology and conservation. Park Ridge, NJ: Noyes Publications.

[7] Zimen, E. 1982. A wolf pack sociogram. Pp. 282-322 In F.H. Harrington and P.C. Paquet eds. Wolves of the World Perspectives of Behavior, Ecology and Conservation. Park Ridge, NJ: Noyes Publications.

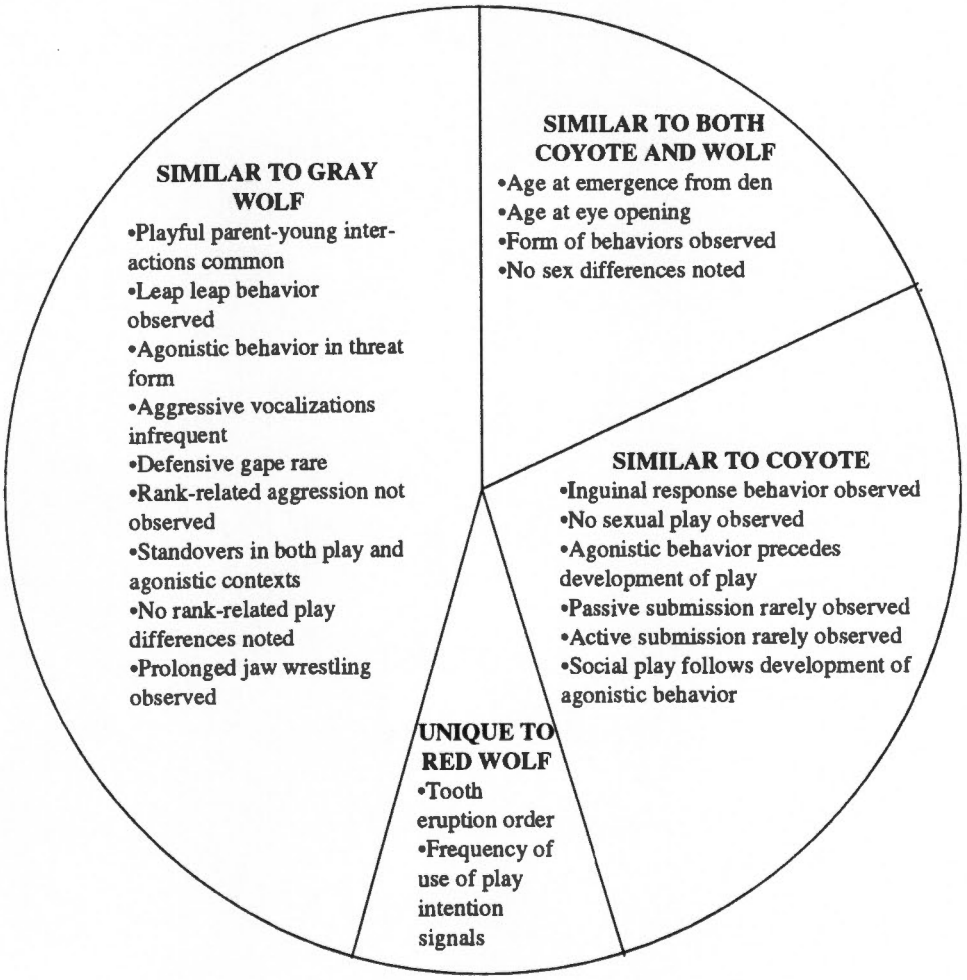

Figure 28. Red wolf behavior observed from 28-50 days of age categorized by similarity to behaviors previously documented in similar age gray wolves and coyotes.

A general discussion of the additional behaviors and events listed in Table 3 will be covered in the respective sections (e.g. development of social behavior, parent-offspring behavior).

Action Patterns

The form of red wolf behavior documented in this study did not differ from that previously reported for both wolves and coyotes (Fox 1971; Bekoff 1972; 1974a; Bekoff 1974b; Bekoff 1978; Mech 1970). Previous studies have indicated that the behavioral repertories of many juvenile and adult canids, as well as their hybrids, are markedly similar (Mech 1970; Fox 1971; Bekoff 1972). While the form of the behavior may not differ, species-specific differences have been identified in the observed frequencies of performance of these same behaviors (Bekoff et al. 1975; 1978). Therefore, several behaviors observed in the current study are worth discussion. The leap leap behavior (Table A-1) has been previously described as a species-specific behavior since it has been documented in wolves and dogs and not in coyotes (Bekoff 1972; 1978). This behavior was observed in the red wolf as a play-solicitor (though not all individuals performed this behavior).

The inguinal response (Table A-1) is an action that has been observed exclusively in coyotes, hybrids with coyote ancestry, and Eastern coyotes (Fox 1971; Bekoff 1972). In the current study, red wolves performed this behavior in response to direct ano-genital stimulation by a pup or adult or direct contact to the inguinal region by another individual or object. In coyotes, the inguinal response has been termed a "behavioral inhibitor"(e.g. when a subordinate animal leans into a more dominant animal during an agonistic interaction, the light inguinal contact elicits an inguinal response from the dominant pup and subsequently terminates the interaction (while performing an inguinal response the animal is generally immobile)). Red wolf pups performing an inguinal response did remain immobile; however, this behavior was observed almost entirely in the context of direct ano-genital (inguinal area) stimulation rather than during agonistic interactions.

The defensive gape (Fox 1970) has also been categorized as a behavior specific to coyotes and not wolves (Table 5). The gape was observed (though relatively infrequently) in both red wolf litters. In all cases, the gape was observed only during serious agonistic encounters. Additionally, one individual in litter 2 performed a "gape-like" behavior which differed qualitatively from that of the others in that the teeth were not exposed.

Jaw wrestling was observed in both litters as a component of wrestle play. Jaw wrestling has previously been observed more frequently in wolves compared to coyotes (Fox 1970).

Ontogeny of Playful and Agonistic Action Patterns

Several trends were noted in the two red wolf litters related to the development of play and aggression. In both litters, agonistic interactions preceded the development of reciprocal play (both as a proportion of all pup-pup social interactions as well as in percentage of time observed). A similar developmental trend has been noted in both wild and captive coyotes (Bekoff 1972; 1974a; 1974b; Bekoff et al. 1975; Fox et al. 1976; Knight 1978; Bekoff 1984) and in a pair of wolf pups (Mech 1970), though some marked differences exist from that observed in the current study. In coyotes, the frequency of agonistic action patterns is highest from days 21-28, declines, and remains relatively stable (and elevated) from days 29-50. Wolves, on the other hand, show increasing levels of agonism from days 21-35 and peak aggression from days 36-42. Furthermore, relative levels of agonistic action patterns in coyotes are higher than that reported for wolves (Bekoff 1974b). The red wolves in this study exhibited peak aggression during days 29-35, though without comparative data from days 21-28, it is not possible to know if agonistic action patterns are decreasing or increasing in frequency at this point (days 29-35). However, since playful action patterns in both litters did not become relatively more frequent than agonistic behaviors until days 36-42, it may be hypothesized that agonistic behaviors peaked during days 29-35, later than that reported for coyotes and earlier than that reported for wolves. Also, the frequency of agonistic interactions remained relatively high in litter 1 rather than decreasing steadily over time as in litter 2.

Despite a peak in levels of agonism, the majority of agonistic encounters observed in the red wolves were in the form of threats and agonistic postures rather than true "fights." Previous studies of coyotes report agonistic action patterns in the form of severe fighting as early as 21 days of age which resulted in clear evidence of a "winner" and "loser" (Table 5; Fox & Clark 1971; Bekoff et al. 1981). Due to the relatively low numbers of true fights in the red wolves, there were insufficient data to quantitatively determine the presence or absence of a dominance hierarchy based on unambiguous markers such as dominations or passive submissive behaviors .

The differences in the frequency of agonistic behaviors between litters could be attributed to both individual and environmental differences; the litter 1 adult male was significantly more aggressive

towards both the pups and the author than the litter 2 male. Also, captive conditions varied between the two sites. The pen which housed litter 1 was bordered by two pens also housing a pair of wolves each, while litter 2 wolves were the only *Canis* species on zoo grounds.

The development of play behavior in the red wolf pups was similar to trends previously observed in coyotes; play-soliciting in the red wolf pups only resulted in reciprocal play following the decline in aggression in both litters (Table 5). In litter 1, where the relative level of aggression remained high, unreciprocated play also remained elevated (more frequent than reciprocal play from days 43-50). In this litter, the prevalent "agonistic atmosphere" was evidenced by the fact that play-solicitors which were given out of sight of the potential play partner (e.g. a leap directed towards another pup while running behind it) were met immediately with threatening postures and action patterns. While statistically significant differences were not found in the ability of pups to solicit play as has been documented previously in coyotes, there appeared to be marked differences among pups in litter 1. The play solicits of some individuals in this litter were routinely met with avoidance, submissive face paws, roll overs and passive submission.

In both litters, play solicitors were used to initiate play a little more than half the time, though the percentage of play bouts preceded by a play solicitor was slightly higher in litter 1. In coyotes, which exhibit a relatively higher proportion of aggressive acts, play solicitors precede play bouts 90% of the time (Table 5; Bekoff et al 1975; Bekoff 1978; 1992). In the red wolf litter that was relatively more "aggressive" (litter 1), play bouts were preceded by play signals slightly more often than in the "more playful" litter 2. While there were no statistically significant differences in the ability to solicit play among pups, more aggressive individuals in both litters did have a harder time successfully soliciting play. On several occasions, a more aggressive pup would perform multiple play solicitors in succession to a potential partner. Each successive attempt was met by increased levels of submission or avoidance. Then, after exhausting their inventory, the soliciting pup would roll over next to its potential playmate (a very vulnerable position) and perform repeated face paws.

In both litters, the type of play observed changed over time and seemed to be correlated to the differential changes in play and aggression. The relative frequency of close contact play (prone and updown) increased throughout development concurrent with the relative increase in play (and decrease in

aggression) for both litters. These changes in play type over time agree with that reported for wolves (Loeven 1993) with the exception of the relative decrease in the proportion of locomotor play in the red wolves. This finding is probably a function of visibility; however, since for both litters, types of contact play were more likely observed due to their stationary nature. Even ambush/stalk play, while initiated by a rush or stalk, usually took the form of contact play following the initial approach.

Object Play

The development of object play also followed the differential development of play and aggression. Object play was observed early in development in both litters, which is consistent to that observed in wolves (Mech 1970; Loeven 1993) and coyotes (Ryden 1975 as cited in Biben 1982). Initially, object play took the form of non social pup-object bouts; the same developmental period during which levels of pup-pup aggression were highest. Additionally, in both litters, the peak frequency of object play occurred during the transitional period in which aggression was decreasing and reciprocal play was increasing (days 43-50 for litter 1; days 36-42 for litter 2). It could be hypothesized that this trend further demonstrates that object play is indeed a form of "play" and not merely vacuum activity since the pups are demonstrating increased "playfulness" at this age.

Social object play (pup-pup-object) only increased in frequency during the time period at which playfulness was most frequent (as a proportion of all social interactions). While outright aggression over objects was not observed in either litter, early approaches to a pup playing with an object were met with defense and avoidance (e.g. taking the object out of reach of the potential play partner) or on rare occasions, threats. In the more playful litter 2, objects were also used as play solicitors. On several occasions in this litter, a pup would terminate a non social object play bout by carrying an object over to a potential playmate and repeatedly pick it up and place it in front of the pup. The adult male in litter 2 was observed to approach a pup engaged in object play on two occasions. While the adult and pup did not engage in any form of social object play (e.g. tug of war), the male proceeded to face paw towards and repeatedly bite the object alongside the pup.

Without comparable data for wolves and coyotes, few direct comparisons on the form of object play between wolves, coyotes and red wolves can be made. However, following Biben's (1982) hypotheses regarding object play and adult sociality, the red wolf follows the "group hunter" pattern by sharing rather

than competing for objects and spending as much time in object-oriented interactions as non-object oriented social interactions. However, as the data from the current study illustrate, data on the ontogeny of object play should also be reviewed in light of the ontogeny of social interactions for a more complete analysis of the variables affecting the form and developmental schedule of object play.

Parent-Offspring Interactions

Consistent with the data reported for other canids, red wolf pups spent significantly more time in proximity to the female than the male throughout the study period (Mech 1970; Ryon 1986; Fentress et al. 1987). In both litters the male also played a significant role in the development of the pups (Ridley 1978; McDonald & Moehlman 1982; Malcolm 1985), though the quality of this role differed between litters. Since general proximity scores were calculated any time that the focal pup was within 5 feet of an adult, the frequency and quality of interactions may be better indicators of the direct impact of parental interactions on the socialization of each litter. For example, female-pup interactions were less frequent than male-pup interactions throughout the entire study period for litter 1, and during days 43-50 for litter 2. The role of the female in both litters was tied directly to the direct provisioning of food (nursing only in both litters) and cleaning/investigation in litter 2. While the male in litter 1 regurgitated to the pups on a daily basis, male-pup interactions were strictly agonistic in nature. In litter 2, no regurgitation was observed (though one unsuccessful attempt was observed by the male) and towards the end of the study period, the male was seeking the proximity of and interacting playfully with pups.

Though correlational, it should be noted that the litter 1 male was more aggressive than litter 2 male (both towards the pups and the author) and the frequency of pup-pup aggression was higher in litter 1 than litter 2. Similarly, litter 2 male was more playful with the pups and the frequency of pup-pup play was higher in litter 2 than litter 1. Additionally, litter 2 adults (both male and female) were remarkably proficient in cleaning the ano-genital region of pups following urination or defecation or in merely investigating the region upon an approach towards a pup. This form of adult-pup behavior was observed more frequently in litter 2 than litter 1. Litter 2 pups also exhibited the pup-pup ano-genital investigation behavior at a much higher frequency than that observed for litter 1. Intraspecific variability in behavior is widespread in carnviores (Fox 1970; Bekoff et al. 1984) though the potential impact of the variability in the quality of adult-pup interactions on the ontogeny of red wolf pup behavior deserves further study.

Potential sources of error in the current study include poor pup visibility at times and the difficulty in discriminating play-fighting from real fighting (compounded by the fact that vocalizations were rarely audible). In captivity, red wolves are housed in naturalistic enclosures which make detailed study of the frequency of specific action patterns very difficult for several reasons. First, distance of the observer from the pups may have contributed to a low frequency of more subtle behavior patterns (e.g. inguinal response, general head and eye changes which indicate play solicitation). Second, as pups moved, especially as they aged and utilized a greater area of the exhibit, they moved in and out of visibility. Interactions may have been incorrectly documented in form and duration if the pair ended an interaction while in view and then moved out of view where the interaction continued and/or changed in motivation.

While the discrimination of agonistic from play sequences many times would not have possible without the detailed data collection from recorded video-tape, many sequences remained difficult to code. A major contributor to this dilemma was the inability to accurately hear vocalizations due to distance from the pups as well as ambient noise. Additionally, play signals are poorly developed when young and more subtle action patterns may have been missed. It is also not known how much the presence of the observer affected the behavior in litter 1. While litter 2 adults habituated quickly to the presence of the observer as well as the general public, litter 1 adults were housed in an off-exhibit area and were more wary of the observer throughout the study. It is not known whether this contributed to the more aggressive nature of the litter.

Conclusions and Recommendations for Future Research

The patterns of physical and behavioral development in the red wolves observed in this study share many similarities with both gray wolves and coyotes (Figure 28). Red wolves exhibited physical development patterns consistent with that reported for other canid species, with the exception of a unique tooth eruption order. Behavioral trends observed in the red wolves were both intermediate to that of coyotes and wolves and shared characteristics of each. The form of pup behavior patterns did not differ qualitatively from that previously documented for either gray wolves or coyotes. However, pups simultaneously exhibited"species-specific" behavior patterns previously attributed to both wolves (leap leap, prolonged jaw wrestling) and coyotes (inguinal response, defensive gape). No unique or potentially "species-specific" behaviors were documented. The time-course of the differential development of play and aggression in the red wolves is also intermediate to that previously documented for coyotes and gray

wolves. While aggressive interactions leading to the wolf dominance hierarchy are commonly not thought to occur until much later in development (post 50 days of age), severe ritualized fights occur early in coyote ontogeny (days 21-28). In the current study, red wolves did not play socially until levels of aggression had declined. However, severe fighting was not observed and therefore insufficient data were available to accurately document that reciprocal social play only occurred once a dominance hierarchy had been established. In sum, the developmental data presented in this study do not support the discrimination of the red wolf from coyotes or wolves on the basis of behavioral ontogeny, nor do they exclude a hybrid origin hypothesis.

Findings in this study demonstrate that non social object play in red wolves is the prevalent form of object play until aggression has declined and reciprocal social play has more fully developed. This form of red wolf object-play may support hypotheses related to species-specific trends of group hunting and living: young red wolves share rather than compete for objects and spend as much time in object-oriented interactions as non-object oriented social interactions. Parent-offspring interaction data indicate that red wolf adult-pup interactions may be more affiliative than that reported in some coyotes and that the male plays a significant role in the development of pups.

Specific areas for future research which were not covered in this study include the development of play and agonistic action patterns from days 21-28 as well as post 50 days of age. Data from these time periods may provide evidence to support the trends seen in this study from days 29-50. Correlates to intra-specific variation and particularly the effect of individual differences in parental behavior on the behavioral development of their offspring also need to be studied. Data from additional subjects are needed to compare to the trends documented in these two litters. Additionally, studies exploring the potential function of the pup-pup ano-genital investigation behavior may provide further insight into the development of early social bonds. In this light, additional research is also needed on the more subtle behaviors associated with dominance. In conclusion, it is hoped that the current study has described preliminary findings related to the ontogeny of red wolf social behavior and that future studies examine both the integrity of these trends as well perform additional comparisons to the closely related wolf and coyote.

Literature Cited

Altman, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227-267.

Atkins, D., and Dillon, L. 1971. Evolution of the cerebellum in the genus *Canis*. Journal of Mammalogy 52(1):96-107.

Bekoff, M. 1972. An ethological study of the development of social interaction in the genus *Canis*: A dyadic analysis. Ph.D. dissert., Washington Univ., St. Louis, Miss.

Bekoff, M. 1974a. Social play and play-soliciting by infant canids. American Zoologist 14:323-340.

Bekoff, M. 1974b. Social play in coyotes, wolves and dogs. BioScience 24:225-230.

Bekoff, M. 1977a. Quantitative studies of three areas of classical ethology: social dominance, behavioral taxonomy and behavioral variability. In: B.A. Hazlett, ed. Quantitative Methods in the Study of Animal Behavior, pp. 1-46. New York: Academic Press.

Bekoff, M. 1977b. Socialization in mammals with an emphasis on nonprimates. In: S. Chevalier-Skohnikoff & F.E. Poirier, eds. Primate Bio-Social Development: Biological, Social and Ecological Determinants, pp. 603-636. New York: Garland Publications, Inc.

Bekoff, M. 1978. Behavioral development in coyotes and Eastern coyotes. In: M. Bekoff, ed. Coyotes: Biology, Behavior and Management, pp. 97-126. New York: Academic Press.

Bekoff, M. 1981. Development of agonistic behaviour: Ethological and ecological aspects. In: P.F. Brain & D. Benton, eds. Multidisciplinary Approaches to Aggression Research, pp. 161-177. Elsevier: North-Holland Biomedical Press.

Bekoff, M. 1984. Social play behavior. BioScience 34:228-233.

Bekoff, M. 1989. Behavioral development of terrestrial carnivores. In: J.L. Gittleman, ed. Carnivore Behavior, Ecology, and Evolution, pp. 89-124. Ithaca, N.Y.: Cornell Univ. Press.

Bekoff, M. 1992. Play signals as punctuation: The structure of social play in canids. Behaviour 132:419-429.

Bekoff, M., and Byers, J.A. 1985. The development of behavior from evolutionary and ecological perspectives in mammals and birds. Evolutionary Biology 19:215-286.

Bekoff, M., and Byers, J.A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: An ethological hornet's nest. In: K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main, eds. Behavioral Development: The Bielefeld Interdisciplinary Project, pp. 296-337. Cambridge: Cambridge Univ. Press.

Bekoff, M., Daniels, T.J., and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191-232.

Bekoff, M., Diamond, J., and Mitton, J.B. 1981. Life-history patterns and sociality in canids: Body size, reproduction, and behavior. Oecologia (Berl) 50:386-390.

Bekoff, M., Hill, H., and Mitton, J.B. 1975. Behavioral taxonomy in canids by discriminant function analyses. Science 190:1223-1225.

Bekoff, M., and Jamieson, R. 1975. Physical development in coyotes (*Canis latrans*), with a comparison to other canids. Journal of Mammalogy 56(3):685-692.

Bekoff, M., and Wells, M.C. 1980a. Social ecology and behavior of coyotes. Adv. Study Behav. 16:252-338.

Bekoff, M., and Wells, M.C. 1980b. The social ecology of coyotes. Scientific American April:130-145.

Biben, M. 1982. Object play and social treatment of prey in bush dogs and crab-eating foxes. Behaviour 79:201-211.

Biben, M. 1983. Comparative ontogeny of social behaviour in three South American canids, the maned wolf, crab-eating fox and bush dog: Implications for sociality. Animal Behavior 31:814-826.

Burghardt, G. 1984. On the origins of play. In: P.K. Smith, ed. Play in Animals and Humans. pp 5-41. Oxford: Basil Blackwell.

Fagen, R. 1981. Animal Play Behavior. New York: Oxford Univ. Press.

Fentress, J.C. and J. Ryon. 1982. A long-term study of distributed pup feeding in captive wolves. Pp. 238-261 In: F.H. Harrington and P.C. Paquet eds. Wolves perspectives of behavior, ecology and conservation. Park Ridge, NJ: Noyes Publications.

Fentress, J.C., Ryon, J. and McLeod, P.J. 1987. Coyote adult-pup interactions in the first 3 months. Canadian Journal of Zoology 65:760-763.

Fox, M.W. 1969. The anatomy of aggression and its ritualization in Canidae: A developmental and comparative study. Behaviour 35:242-258.

Fox, M.W. 1970. A comparative study of the development of facial expressions in canids; wolf, coyote and foxes. Behaviour 36:49-73.

Fox, M.W. 1971. Behaviour of Wolves, Dogs and Related Canids. Malabar, Fla.: Robert E. Krieger Publishing Company, Inc.

Fox, M.W. 1978. The Dog: Its Domestication and Behavior. New York: Garland STMP Press.

Fox, M.W., and Clark, A.L. 1971. The development and temporal sequencing of agonistic behavior in the coyote (*Canis latrans*). Zeitscrift fur Tierpsychologie 28:262-278.

Fox, M.W., Halperin, S., Wise, A., and Kohn, E. 1976. Species and hybrid differences in frequencies of

play and agonistic actions in canids. Zeitscrift fur Tierpsychologie 40:194-209.

Gittleman, J.L. and S.L. Pimm. 1991. Crying wolf in North America. Nature 351: 524-525.

Goldman, E. A. 1937. The wolves of North America. Journal of Mammalogy 18: 37-45.

Hofer, P.H. 1981. Parental contributions to the development of their offspring. In: D. J. Gubernick and P.H. Klopher, eds. Parental Care in Mammals, pp. 77-115. New York: Plenum Press.

Kleiman, D. 1967. Some aspects of social behavior in the Canidae. American Zoologist 7:365-372.

Kleiman, D. and J.R. Malcolm. 1981. The evolution of male parental investment in mammals. In: D. J. Gubernick and P.H. Klopher, eds. Parental Care in Mammals, pp.347-387. New York: Plenum Press.

Klopfer, P.H. 1981. Origins of parental care In: D. J. Gubernick and P.H. Klopher, eds. Parental Care in Mammals, pp. 1-12. New York: Plenum Press.

Knight, S.W. 1978. Dominance hierarchies of captive coyote litters. M.S. thesis, Utah State Univ., Logan, Utah.

Lawrence, B., and Bossert, W. 1967. Multiple character analysis of *Canis lupus, latrans,* and *familiaris,* with a discussion of the relationships of *Canis niger*. American Zoologist 7:223-232.

Lehner, P.N. 1978. Coyote Communication. In: M. Bekoff, ed. Coyotes: Biology, Behavior and Management, pp. 127-162. New York: Academic Press.

Lehner, P.N. 1996. Handbook of Ethological Methods (2nd. ed.) Cambridge: Cambridge Univ. Press.

Lindsey, S.L. 1987. The effect of food availability on the social organization and behavior of captive coyotes (*Canis latrans*). Ph. D. dissert., Colorado State Univ., Fort Collins, Col.

Loeven, J.C. 1993. The ontogeny of social play in timber wolves, *Canis lupus*. M.S. thesis, Dalhousie Univ., Halifax, Nova Scotia.

Loizos, C. 1966. Play in mammals. Symp. Zool. Soc. Lond. 18:1-9.

Lyndaker, S.M. 1978. The development of begging and regurgitation in gray wolf (*Canis lupus*) pups. M.A. thesis, Southern Illinois Univ., Carbondale, Ill.

Macdonald, D.W., and Moehlman, P.D. 1982. Cooperation, altruism and restraint in the reproduction of carnivores. In: P.P.G. Bateson & P.H. Klopfer, eds. Perspectives in Ethology (vol 5-Ontogeny), pp. 433-467. New York: Plenum Press.

Malcolm, J.R. 1985. Parental care in canids. American Zoologist 25:853-856.

Malm, K., and Jensen, P. 1993. Regurgitation as a weaning strategy — a selective review on an old subject in a new light. Applied Animal Behaviour Science 36:47-64.

Martin, P. 1984. The (four) whys and wherefores of play in cats: A review of functional, evolutionary, developmental and causal issues. Pp. 71-94 In P.K.Smith, ed. Play in Animals and Humans New York: Basil Blackwell.

Mech, L. D. 1970. The Wolf: Ecology of an Endangered Species. New York: Natural History Press.

O'Brien, S.J. and E. Mayr. 1991. Bureaucratic mischief: Recognizing endangered species and subspecies. Science 251: 1187-1188.

Paradiso, J. L. and R. M. Nowak. 1971. A report on the taxonomic status and distribution of the red wolf. U.S.D.I. Spec. Sce. Rep. Wildl. #145. 36 pp.

Paradiso, J. L. and R. M. Nowak. 1972. *Canis rufus*. Mammalian Species Report Number 22: 1-4.

Phillips, M.K. and V. G. Henry. 1992. Comments on red wolf taxonomy. Conservation Biology 6: 596-599.

Rasa, O.A.E. 1971. Social interaction and object manipulation in weaned pups of the Northern elephant seal (*Mirounga angustirostris*). Zeitscrift fur Tierpsychologie 29:82-102.

Ridley, M. 1978. Paternal care. Animal Behavior 26:904-932.

Roy, M.S., Geffen, E., Smith, D. Ostrander, E. and Wayne, R.K. 1994. Patterns of differentiation and hybridization in North American wolf-like canids revealed by analysis of microsatellite loci. Mol. Biol. Evol. 11: 553-570.

Ryon, J. 1986. Den digging and pup care in captive coyotes. Canadian Journal of Zoology 64:1582-1585.

Scott, J.P. 1967. The evolution of social behavior in dogs and wolves. American Zoologist 7:373-381.

Scott, J..P. and Fuller, J. L. 1965. Genetics and the Social Behavior of the Dog. Chicago: University of Chicago Press.

Siegel, S. 1956. Nonparametric Statistics: For the Behavioral Sciences. New York: McGraw-Hill Book Company, Inc.

Shaw, J.H. 1975. Ecology, behavior and systematics of the red wolf (*Canis rufus*). Ph.D. dissert., Yale University.

Silver, H., and Silver, W.T. 1969. Growth and behavior of the coyote-like canid of Northern New England with observations of canid hybrids. Wildlife Monographs 17:1-40.

Snow, C.J. 1967. Some observations on the behavioral and morphological development of coyote pups. American Zoologist 7:353-355.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. New York: W.H. Freeman and Company.

Wayne, R.K., and Gittleman, J.L. 1995. The problematic red wolf. Scientific American July:36-39.

Wayne, R.K. and Jenks, S.M. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. Nature 351: 565-568.

Willkomm, S. 1990. Quantitative analysis of the ontogeny of play behaviour in canid hybrids. Ethology 86:287-302.

Zimen, E. 1982. A wolf pack sociogram. Pp. 282-322 In F.H. Harrington and P.C. Paquet eds. Wolves of the World Perspectives of Behavior, Ecology and Conservation. Park Ridge, NJ: Noyes Publications.

Appendix

Table A-1. Captive red wolf ontogeny ethogram. Behaviors derived from personal observation (T. Wagener) as well as modified and adapted from published canid ethograms including Loeven (1993); Bekoff (1974); Knight (1978); Lyndaker (1978) and Lindsey (1987). Codes used during scoring are indicated within ( ). Behaviors preceded by an * were observed in both playful and agonistic interactions. However, the behavior is categorized by the most frequently observed motivational context.

AGONISTIC BEHAVIOR

States

Agonistic(AN)	Social interaction marked by either a full fight (see below) or reciprocal threatening body positions including the presence of one or more of the following: a stiff erect posture, threatening facial expression and/or aggressive vocalization.
Fight (FI)	An interaction in which subject approaches another followed by mutual growl--ing, threatening and biting. This is followed by both subjects growling, rising onto their hind legs and batting at each other with the forepaws or grasping each other around the neck or shoulders (sparring), growling, threatening, and each attempting to pin the other to the ground. Interactions in which only one subject used these behaviors were scored as attacks (see Event Behaviors) rather than fights. Fights which ended with neither subject rolling onto its back or side to signal submission (rollover) were called unresolved fights. Behaviors per formed during a fight were scored for frequency only.

Events

Attack (AT)	Subject approaches another with growling, threatening and biting. May be followed by subject rising on its hind legs and batting at the other with its forepaws. If behaviors are reciprocated, scored as a fight.
Aggressive Vocalization (AV)	Growl.
Back arch (BA)	Subject raises its back while standing; observed during or immediately follow-

	-ing an agonistic interaction.
*Complete Standover (SO)	Subject places its forelegs (completely extended) on another between the front and hindquarters and attempts to remain over the recipient if it tries to move. Usually preceded by a chin rest. Scored by food context also (within 1.5 feet of food source or not).
Distress Vocalization (DV)	Whining or high-pitched yelping usually associated with agonistic interactions. Not scored as a distress vocalization if accompanying soliciting.
Domination (DO)	An agonistic interaction in which one or both subjects performed agonistic behaviors (aggressive vocalizations, threats, hipslams, bites etc.) and one sub--ject rolled over onto its side or back (the rollover).
Gape (DG)	Facial expression characterized by open mouth and retracted lips; observed in defensive agonistic contexts.
Grin (GR)	Facial expression in which subjects slightly opens mouth horizontally exposing teeth; observed in submissive agonistic contexts.
Hip Slam (HS)	Subject swings its hips towards another and uses the motion to terminate the interaction or displace the recipient. Observed during agonistic interactions.
*Incomplete Standover (IS)	Subject places its forelegs (not fully extended) on another between the front and hindquarters and attempts to remain over it if the recipient tries to move. Many times preceded by a chin rest. Scored by food context also (within 1.5 feet of food source or not).
Mount (MT)	Subject stands behind another and rests on its back with its forepaws clasped around the recipient's midsection or pelvic region.

*Rollover (RO)	Subject falls or lies on its side or back with hind legs raised and ears back. Scored as passive, active or play fight to indicate the context.

AFFILIATIVE BEHAVIOR

States

Follow (FO)	Subject locomotes directly behind another
Interaction (IN)	An interaction which is ambiguous in context; not clearly play or agonistic in nature.
Play (PL)	An interaction which is marked by the reciprocal use of at least one of the following behaviors: approach/withdrawal, exaggerated approach, face paw, leap, leap leap, play bow, tail wag approach and face, scruff or general body bites. Behaviors performed during a play bout were scored for frequency only. Play was categorized as ambush/stalk, locomotor, one up/onedown, multiple actor, wrestle or unreciprocated (see definitions below). Interaction may seem purposeless, action patterns from other contexts may be used and temporal sequencing may be altered (Bekoff 1984)
Play-ambush/stalk (PL-AM)	Subject either (1) lies or sits in one place, stares at another, and then pounces or rushes when it the recipient approaches or (2) takes slow, deliberate steps towards another with its body held close to the ground. Scored as ambush/stalk play only if the recipient responds; scored as unreciprocated play if it does not.
Play-locomotor (PL-LO)	Subjects run, trot or walk together, around or in pursuit of each other occasionally making body contact. The interaction is scored as locomotor if only 1 contact is made between locomotions. Scored as contact play if > or = 2 contacts are made in succession with no locomotion between them.
Play-one up/down	Play type in which one subject is standing or sitting with the fore and/or back

(PL-UP)	legs extended while the other is prone.
Play-multiple actor (PL-MA)	Play type involving more than two participants.
Play-wrestle (PL-WR)	Play type in which subjects are sitting, standing or moving around each other while making frequent body contact.
Unreciprocated Play (UP)	Subject directs any play intention behaviors (see designated Event Behaviors below) towards another who does not respond, tries to avoid the initiator, or becomes aggressive. If both pups used aggressive actions following the play initiator, the interaction was also scored as agonistic.

Events

*Ano-genital Investigation(GI)	Subject investigates the ano-genital region of another by either sniffing (genital inspect) or licking (genital lick). The latter was only scored if licking was clearly observed. If the interaction was clearly agonistic, it was scored as such though the any genital licking was scored as well.
Approach (AP)	Subject locomotes toward another with its attention clearly directed towards it.
Approach/Withdrawal (WI)	Play initiator in which subject approaches another immediately followed by a movement demonstrating physical intent to move away (e. g. rock back and forth).
Chin rest (CR)	Subject rests its chin on the back of another. Observed during a contactual cir--cle or immediately prior to a standover.
Clasp (CL)	Subject grasps another's midsection and/or pelvic region with its forepaws; dis--tinguished from a mount in that orientation is not always from behind the recipient.

Contactual circle (CC)	Interaction in which two pups circle each other while in close contact usually performing concurrent chin rests.
Exaggerated Approach (EA)	Play initiator in which subject approaches another with a bouncy gait or a rush; head and shoulders are frequently moved from side to side.
*Face bite (FB)	Subject directs bite or bite intention towards another's face area.
Face bump (BU)	Following a leap towards another, subject bumps into the body of another with its face.
Face lick (FL)	Subject licks the face of another. Scored only if contact is made.
*Face paw (PA)	Subject uses foreleg to strike at/towards face or body of another; scored as pas--sive, submissive or play fight context.
*General Body Bite (GB)	Subject directs bite or bite intention towards another's body.
*Headshake (SK)	Subject moves head vigorously from side to side while biting (full or inhibited) another.
*Lean (LN)	Subject uses its body to push against another; subjects are generally immobile otherwise. Action may result in the recipient being pushed off balance.
Leap (LP)	Play initiator in which subject jumps into the air (all four legs) as it approaches another.
Leap leap (LL)	A play initiator in which the subject jumps up into the air 2 times as it approaches another. Previously demonstrated to potentially be a species-specific action pattern (Bekoff, 1974).

Play Bow (BO)	Play initiator in which subject crouches on forelegs while elevating its rear legs.
*Scruff Bite (SB)	Subject directs bite or bite intention towards another's shoulder area.
Tail Wag (TW)	Subject is standing and not moving, yet tail is moving horizontally from side to side. Attention is usually directed towards another.
Tail Wag Approach (TA)	Subject locomotes towards another while moving tail horizontally from side to side.
*Terminate (TE)	Subject terminates an interaction by turning or locomoting away from another or becoming immobile.

ADULT-PUP BEHAVIOR

States

Affiliatory (M-AF or F-AF)	Adult-pup interaction which included any of the following behaviors: play-soliciting, pup to adult general body bites, muzzle-muzzle contact or face-licking.
Agonistic/Disciplinary (M-BI or F-BI)	Adult-pup interaction which an adult directs at least one full or inhibited disciplinary bite towards a pup.
Investigation (M-IN or F-IN)	Adult-pup interaction in which adult (male or female) performs an ano-genital lick or investigation towards a pup.
Nurse (NU)	Subject is consuming milk from the dam.
Proximity (PR)	Subject is within 1 adult body length (approximately 5 feet) of another. Scored as proximity-female (PF), proximity-male (PM), proximity-both (PB)or no proximity (PN).

Solicit (ST) — Subject follows dam or sire while repeatedly jumping towards their muzzle and/or whining.

Events

*Inguinal Response (IR) — Subject either lifts its hindleg off the ground or rotates it slightly following contact to the inguinal region. Scored only if observed during a pup-pup interaction, not during an adult-pup interaction such as anal-genital cleaning by the adult.

Regurgitation (RE) — Subject vomits food, which is consumed by others.

OBJECT-ORIENTED BEHAVIOR

States

Object Play (Social) (OS) — More than one subject plays with an inanimate object .Behavioral events performed during an object play bout include toss, carry, bite, paw, shake, leap, approach/withdraw, play bow, and tug-of-war. If two subjects were playing with the same object yet attention was clearly directed towards the object exclu--sively, the bout was scored as object play-non social.

Object Play (Non social) (ON) — Subject is playing with an inanimate object by itself, or if with others, its attention is towards the object and not the other subjects. .Behavioral events performed during an object play bout include toss, carry, bite, paw, shake, leap, approach/withdraw, and play bow.

Events

Carry (CA) — Subject locomotes while holding an object in its mouth.

Toss (T0) — Subject throws object from its mouth by moving its head upwards quickly.

Tug-of-war (TG) — Subject holds object in its mouth while another grasps object and subjects pull

in opposite directions (scored in Object Play-Social).

GENERAL ACTIVITY

States

Den (DE)	Subject is inside artificial den structure; out of sight.
Eat (ET)	Subject consumes dry dog food.
Explore (EX)	Subject is alternatively locomoting, pawing and/or sniffing an object or general area.
Locomote (LO)	Subject moving at either a walk, trot or run.
Not Visible (NV)	Subject is not visible due to distance, lighting, tree or vegetation, etc.
Other (OT)	Subject performs a behavior not covered by any other state category (most fre--quent other behaviors included standing, sitting, and self groom)
Self Play (SP)	Subject chases its own tail, bites its own limb(s), etc.
Sleep (SL)	Subject lying down, unmoving with eyes closed.

Events

Over Mark (OM)	Subject urinates or defecates over the area in which another previously urinated or defecated.
Pass (PA)	Subject locomotes near another (within 1 body length) which is also locomoting but in an opposite direction; animals do not interact.
Scrape Mark (SM)	Subject uses its front and/or back paws to tear at the ground. Usually observed following urination or defecation.

Urinate (UR)	Subject expels urine.

Table A-2. The median frequency of behavior patterns observed in individual captive red wolves from 29-35 days of age.

ID	Sex	Behavior [1]															
		AN [2]	PL [2]	UN [2]	IN [2]	PS [2]	ON [3]	OS [3]	PF [4]	PM [4]	PB [4]	F-IN [5]	M-IN [5]	F-BI [5]	M-BI [5]	F-AF [5]	M-AF [5]
H	F	.76	.00	.00	.10	.00	.50	.00	16.27	5.10	.00	.60	.20	.00	.00	.00	.00
S	M	.27	.18	.00	.00	.55	.00	.00	.17	.63	.00	.00	.00	.00	.00	.00	.00
B	M	.29	.10	.20	.42	.29	1.00	.00	51.73	3.56	10.38	.20	.00	.50	.00	.00	.00
U	M	.29	.15	.29	.29	.17	1.00	.00	16.35	6.23	.00	.75	.33	.00	.00	.10	.00
B2	F	.14	.12	.00	.04	.26	0.00	0.00	4.20	7.45	3.43	.00	.75	.00	.00	.00	.25
F	M	.29	.00	.18	.00	.26	0.50	0.00	16.40	0.78	7.25	.61	.00	.05	.00	.00	.00
J	M	.18	.13	.00	.00	.33	0.00	0.00	30.10	0.00	0.00	.00	1.00	.00	.00	.00	.00
T	F	.38	.27	.21	.13	.17	0.00	0.00	9.50	2.69	0.00	.00	.50	.13	.00	.00	.10
U2	M	.43	.33	.18	.11	.00	0.00	0.00	26.13	4.69	2.10	.50	.00	.10	.00	.00	.00

[1] See Table A-1 and Chapter 2 for behavior definitions.

[2] Expressed as a median proportion of all pup-pup social interactions

[3] Expressed a a median proportion of all pup-object play

[4] Expressed as a median duration (s) in proximity to adult(s)

[5] Expressed as a median proportion of all adult-pup interactions, i.e. the proportion of all adult-male interactions that included either a disciplinary bite (M-BI), investigation (M-IN) or affiliatory behavior (M-AF)

Table A-3. The median frequency of behavior patterns observed in individual captive red wolves from 36-42 days of age.

ID	Sex	Behavior [1]															
		AN [2]	PL [2]	UN [2]	IN [2]	PS [2]	ON [3]	OS [3]	PF [4]	PM [4]	PB [4]	F-IN [5]	M-IN [5]	F-BI [5]	M-BI [5]	F-AF [5]	M-AF [5]
H	Female	.07	.51	.05	.40	.53	.50	.00	8.19	4.61	3.34	.50	.00	.00	.00	.50	.00
S	Male	.20	.33	.20	.33	.33	1.00	.00	23.33	8.18	.00	.00	.00	.00	.00	.00	.20
B	Male	.29	.44	.00	.14	.57	1.00	.00	28.68	.00	.61	.20	.75	.20	.00	.00	.00
U	Male	.18	.50	.00	.21	.58	.50	.00	7.25	4.23	.73	.00	.50	.20	.10	.50	.20
B2	Female	.00	.25	.50	.33	.67	.00	.00	6.34	.49	.00	.00	.00	.00	.00	.00	.00
F	Male	.13	.13	.50	.25	.63	.50	.00	47.09	.50	.00	.00	.00	.00	.00	.00	.00
J	Male	.75	.00	.13	.13	.13	.00	.00	23.67	.19	.00	.50	.00	.00	.00	.00	.00
T	Female	.08	.38	.13	.00	.75	.00	.00	7.68	.40	.00	.00	.00	.00	.00	.00	.00
U2	Male	.38	.13	.13	.27	.31	.00	.00	4.60	4.20	.00	.00	1.00	.00	.00	.00	.00

[1] See Table A-1 and Chapter 2 for behavior definitions.

[2] Expressed as a median proportion of all pup-pup social interactions

[3] Expressed a a median proportion of all pup-object play

[4] Expressed as a median duration (s) in proximity to adult(s)

[5] Expressed as a median proportion of all adult-pup interactions, i.e. the proportion of all adult-male interactions that included either a disciplinary bite (M-BI), investigation (M-IN) or affiliatory behavior (M-AF)

Table A-4. The median frequency of behavior patterns observed in individual captive red wolves from 43-50 days of age.

ID	Sex	Behavior															
		AN	PL	UN	IN	PS	ON	OS	PF	PM	PB	F-IN	M-IN	F-BI	M-BI	F-AF	M-AF
H	Female	.00	.67	.00	.33	.67	1.00	.00	42.52	.00	.00	.00	.00	.00	.00	.00	.00
S	Male	.11	.75	.00	.00	.89	.50	.20	3.76	24.22	.00	.00	.14	.00	.50	.00	.00
B	Male	.23	.43	.00	.29	.50	.50	.00	28.08	8.52	.65	.00	.00	.00	.25	1.00	.00
U	Male	.00	.50	.04	.29	.54	.50	.00	4.54	7.07	.61	.00	.00	.00	.00	.00	.00
B2	Female	.00	.50	.25	.00	.50	.67	.00	30.77	13.73	2.13	.00	.00	.00	.00	.00	.00
F	Male	.00	.00	.50	.50	.50	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
J	Male	.40	.00	.00	.00	.43	.00	.00	.00	11.04	.00	.00	.00	.00	.00	.00	.00
T	Female	.33	.06	.25	.33	.35	.58	.17	.00	.00	.00	.00	.00	.00	.00	.00	.00
U2	Male	.13	.13	.10	.00	.63	1.00	1.00	.36	1.40	.00	.00	.00	.00	.00	.00	.00

1 See Table A-1 and Chapter 2 for behavior definitions.

2 Expressed as a median proportion of all pup-pup social interactions

3 Expressed a a median proportion of all pup-object play

4 Expressed as a median duration (s) in proximity to adult(s)

5 Expressed as a median proportion of all adult-pup interactions, i.e. the proportion of all adult-male interactions that included either a disciplinary bite (M-BI), investigation (M-IN) or affiliatory behavior (M-AF)

Vita

Tarren Wagener was born in Bethlehem, Pennsylvania on January 31, 1967. She attended public schools in several places, including Staunton, Virginia; Durham, North Carolina; and Fairfax County, Virginia. She graduated from South Lakes High School in Reston, Virginia in 1985. Following graduation, she entered Virginia Polytechnic Institute and State University (Virginia Tech) in Fall 1985 as an Animal Science/Pre-Vet major. In Spring, 1987, she left the University to pursue a managerial position at a small zoological facility in Fairfax County, Virginia. In Fall 1987, she returned to Virginia Tech to complete her degree and in May, 1990, received a B.S. in Psychology with a minor in Animal Science. Following graduation, she enrolled in the Master's degree program in Animal Behavior at Bucknell University in Lewisburg, Pennsylvania. Prior to completing her degree, she transferred to the University of Tennessee as a graduate student in Ethology. After receiving funding from the U.S.F.W.S. for the red wolf research project, she was offered a position at the Fort Worth Zoo in Fort Worth, Texas. In 1993, she left the University to accept a position as Conservation Assistant in the new Conservation Department at the Zoo. While working full-time in Texas, she completed her thesis research and in December 1998, received the Master's degree in Ethology from the University of Tennessee, Knoxville.

She is currently employed by the Fort Worth Zoo as Conservation Science Manager and is responsible for both the coordination of the Zoo's research activities as well as the development of a zoo-wide animal training and enrichment program. She participates in numerous national conservation programs and is actively involved with zoo-based wolf (*Canis lupus baileyi, Canis rufus*), lion (*Panthera leo*), and white rhino (*Ceratotherium simum*) conservation initiatives. She serves as Coordinator for both the Lion Species Survival Plan (SSP), a national cooperative conservation program for the species, as well as zoo-based efforts for the United States swift fox (*Vulpes velox*).